BETWEEN-PATCH MOVEMENT BEHAVIOUR OF JUVENILE ATLANTIC COD (GADUS MORHUA)

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BETWEEN-PATCH MOVEMENT BEHAVIOUR OF JUVENILE ATLANTIC COD (*GADUS MORHUA*)

by

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Abstract

Complex habitat provides a predator refuge for many animals. When such habitat is fragmented, movement between patches may be driven by many factors including foraging opportunities, density effects, abiotic factors, and predator distribution. Although the effects of these factors are well-studied in terrestrial environments, few studies have focussed on inter-patch movement in the marine environment beyond the role of foraging success in patch selection and departure. I examined the effects of release density, gap distance, and predator presence on the inter-patch movements of juvenile Atlantic cod (*Gadus morhua*) in a 12 m by 3 m raceway tank containing patches of artificial eelgrass. In addition to the main factors examined, I also collected data to test the effects of fish length and average group size on between-patch movement. Results show that between-patch distance and predator location each have significant effects on the total number of times juvenile Atlantic cod cross gaps in complex habitat. Interactions among experimental conditions had significant effects on the time taken to depart the release patch, and on the duration of the first completed between-patch movement. I also conducted mark-recapture experiments in Newman Sound, Terra Nova National Park. In 2006, I released 348 juvenile Greenland cod (*Gadus ogac*) into artificial eelgrass patches following tagging with visual implant alphanumeric tags (VI Alpha™). In 2007, I released 450 juvenile Atlantic cod, also tagged with VI Alpha tags into artificial eelgrass patches. Because of low recovery rates, I was unable to confirm laboratory findings in the field. However, I was able to demonstrate that standard length negatively affects recapture of juvenile Atlantic cod, and that the presence of conspecifics affects the movement of juvenile Atlantic cod in highly fragmented habitat. My laboratory and field results indicate that the inter-patch movements of fishes may be determined by several factors other than foraging success, and that movement decisions in juvenile cod are based on evaluation of multiple risks and benefits.

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Chapter 1: Animal movement in fragmented landscapes: application of terrestrial concepts to marine environments

The patchy distribution of suitable animal habitat has the potential to modify all aspects of animal behaviour, from foraging to reproductive success. Fragmentation of preferred habitat into smaller, geographically isolated patches can have numerous effects on animal behaviour and has potential consequences for population dynamics (Andrén 1994). Natural and anthropogenic disturbances are potential causes of habitat fragmentation and their effects may occur at varying spatial scales. Fragmentation at different spatial scales has variable effects on different species, depending on the movement capabilities of the animals in question (Andrén 1994), and such effects have been studied in numerous terrestrial species (Desrochers and Hannon 1997, Zollner and Lima 1999, Grubb Jr. and Doherty Jr. 1999, Norris and Stutchbury 2002, Bélisle and Desrochers 2002, Bowman and Fahrig 2002, Kie et al. 2005, Bosschieter and Goedhart 2005). Similarly, increased animal movement between areas of fragmented habitat has led to the concept of movement corridors, which have been examined for their conservation potential using both experimental and theoretical approaches (Beier 1993, Tischendorf and Wissel 1997, Beier and Noss 1998, Gilliam and Fraser 2001, Tull and Krausman 2001, Baker 2007, Graves et al. 2007). The effects of habitat fragmentation on marine species are less understood than their terrestrial counterparts, but may have similar implications for animal movement decisions.

I apply experimental approaches similar to those used in terrestrial landscape ecology to juvenile cold-water marine fish in order to test the effects of habitat

fragmentation on movement in a coastal marine habitat. In this chapter, I present information on habitat associations and between-patch movement in terrestrial and marine systems, followed by information on the study system I used in my experiments. In Chapter 2, I present my results from laboratory experiments that identify specific factors that affect between-patch movement behaviour in juvenile Atlantic cod *Gadus morhua*. To determine if habitat gaps present a barrier to movement in a natural setting, I conducted field experiments to describe juvenile cod movement in fragmented habitat. I present these experiments in Chapter 3. In Chapter 4, I discuss the implications of my field and laboratory work and the applicability of some key terrestrial landscape ecology concepts to marine systems.

I apply both lab and field studies to address the potential shortcomings of using a single approach. Laboratory studies, while providing greater control over individual experimental factors, may produce misleading results due to artificiality in the conditions experimental animals are exposed to (Magurran et al. 1996). Conversely, field experiments provide natural conditions for experimental animals however it can be difficult to isolate the factors responsible for producing a given result (see Smith 1997).

1.2. Physical complexity and predation risk

The physical structure of habitat plays a large role in the behaviour of animals through modification of predation risk. The nature of this modification is largely dependent on the species and habitat in question. For some organisms, physical structure may increase risk of predation by impeding the ability of animals to detect

approaching predators. Animals that experience a decrease in their ability to detect predators in complex habitat may increase vigilance behaviour, an effect that can be seen in greater rhea *Rhea americana* (Martella et al. 1995) and Dall sheep *Ovis dalli dalli* (Frid 1997). For other species, such as finches, complex habitat may be both a source of predation risk and a potential refuge from predation, creating a trade-off between foraging too close to, or too far from, forested areas (Lima et al. 1987). Predation risk may also be reduced in physically complex habitat (reviewed by Lima and Dill 1990). Numerous studies on the nature of this relationship and the potential consequences for animal behaviour have been conducted on both terrestrial and aquatic species, with a large degree of similarity between the two groups in their use of complex habitat. Wild guinea pigs *Cavia aperea* use high, dense vegetation as protection from predators (Rood 1972), and increase their scanning behaviour when foraging at larger distances from such cover, suggesting increased distance from complex habitat increases the risk for these animals (Cassini 1991). Similarly, grey squirrels *Sciurus carolinensis* use trees as protective cover from predators (Newman et al. 1988). When presented with food at various distances from such cover, grey squirrels eat faster, move more quickly between food patches, and handle food faster, suggesting an increase in perceived risk for these animals as distance from cover increases (Newman et al. 1988).

Studies of desert rodents show that they may use protective habitat differently, depending on their own vulnerability to predation. Species that are more vulnerable to predators use complex habitat in the form of bushes more often than less vulnerable species (Kotler 1984). Use of complex cover by rodents may also vary depending on

the nature of the cover available, in that some species are less vulnerable to predation in areas of vertical cover (Wywialowski 1987). Despite evidence from Lima et al. (1987) on the variable risk presented by protective cover, many other studies show that birds use complex habitat as refuge from predators. White crowned sparrows *Zonotrichia leucophry* (Lima 1990), willow tits *Parus montanus* (Hogstad 1986) and white-throated sparrows *Zonotrichia albicollis* (Schneider 1984) all use trees as protective cover from predators.

Work on freshwater aquatic species shows that complex habitat in aquatic environments also provides protection from predators. Bluegill sunfish *Lepomis macrochirus* (Savino and Stein 1982, Gotceitas and Colgan 1989) experience reduced predator encounter rates in complex habitat, and predation by water bugs on tadpoles *Dendropsophus minutus* is reduced in vegetation (Kopp 2006). Studies that show reduced predation risk for freshwater species in vegetated habitats demonstrate that complex habitat can have a functional role in aquatic environments similar to that of terrestrial systems. While less numerous than similar studies in freshwater and terrestrial systems, research on marine species since the review of Lima and Dill (1990) show that complex habitat in this environment may also reduce predation risk. Density of cunner *Tautogolabrus adspersus* increases and predation rates decrease as habitat becomes more complex (Tupper and Boutilier 1997). Juvenile Atlantic cod in eelgrass are subject to lower predation rates than those outside of eelgrass habitat (Linehan et al. 2001) and predation rates in larger patches are lower than in smaller patches (Laurel et al. 2003b). Sogard and Olla (1993) showed that juvenile walleye pollock *Theragra chalcogrammu* enter artificial seagrass habitat when in the presence

of predators, in contrast to their use of open areas when predators are absent. As can be seen above, complex habitat provides protection from predators for many animal taxa, thereby providing increased incentive to associate with complex areas.

1.3 Between-patch movement, a terrestrial perspective

Although association with complex habitat provides refuge from predation for many species, physically complex habitat is not uniform in space. Fragmentation of complex habitats into variously-sized patches increases the likelihood that movements between patches may be necessary. Potential reasons for movement may include resource depletion, predator presence, changing environmental conditions, seasonal migration, and mating behaviour. Work on between-patch movement, or "gap crossing" (as it is generally referred to in the terrestrial literature), has focused predominantly on terrestrial species. Studies on songbirds have shown multiple responses to habitat gaps that indicate a preference for avoidance of open areas. Desrochers and Hannon (1997) showed that songbirds will preferentially select longer routes that allow them to stay within forested areas over shorter routes that expose them to open areas. They also showed that the response to gaps in habitat may be species specific (Desrochers and Hannon 1997). Reed warblers *Acrocephalus scirpaceus* forced to fly through gaps in habitat choose the shortest possible gap to complex habitat, and are reluctant to cross gaps larger than 50 m (Bosschieter and Goedhart 2005). Chickadees and warblers choose longer, more convoluted routes through forest cover, rather than utilizing shorter, direct routes through open areas in the canopy (Desrochers and Hannon 1997, Bélisle and Desrochers 2002, Creegan and

Osborne 2005). The study by Bélisle and Desrochers (2002) also examined the potential effects of group size on gap crossing behaviour, and showed that there was no effect of conspecific group size on between-patch movements. The reluctance of bird species to cross open areas may have implications for connectivity between groups of birds distributed among isolated areas of suitable habitat, and Bosschieter and Goedhart (2005) suggested that corridors characterized by small gaps could facilitate movements between areas of suitable habitat. Movement across gaps in habitat may affect males and females differently. Norris and Stutchbury (2002) showed that female hooded warblers *Wilsonia citrina* make fewer forays into non-forested areas and may be more restricted in areas of high fragmentation than males during the breeding season.

In addition to the effects of habitat gaps on bird behaviour, there are other species that appear to be susceptible to fragmentation of habitat. Studies of dormice *Muscardinus avellanarius* show that even narrow (1 m) gaps in habitat may represent a barrier to movement (Bright 1998). Male root voles *Microtus oeconomus* decrease movement rates when exposed to habitat gaps 4 m wide, but not when exposed to smaller gaps (Andreassen et al. 1996), suggesting that gap dynamics are fluid in their effects on some species. White footed mice *Peromyscus leucopus* choose routes through open areas during times of higher light levels when their perceptual range is increased, but move along these routes during the night, when vulnerability to predation in open areas is diminished (Zollner and Lima 1999). The movement of jumping spiders *Phidippus princeps* is reduced when there are open areas between habitat patches (Baker 2007), showing that hesitancy to cross habitat gaps is not

limited to vertebrate species. Gap-crossing behaviour may also be mediated by the quality of habitats on each side of the gap. Density of trees modifies the response of deermice *Peromyscus maniculatus* moving in either continuous or discontinuous habitat (Ruefenacht and Knight 1995). Chipmunks *Tamias striatus* do not appear to be limited by gaps in complex habitat (Bowman and Fahrig 2002). Thus, gaps in habitat clearly do not affect all animals in the same way.

Disruption of animal movement by habitat fragmentation has also been studied from the perspective of increasing connectivity between populations that have been or may become separated by habitat fragmentation. Global Positioning Systems (GPS) have been used to identify functional corridors for brown bears *Ursus arctos*, suggesting that certain landscape features should be preserved to facilitate movement (Graves et al. 2007). Simulations of cougar *Felis concolor* connectivity and the application of those simulations to cougars in California suggest that corridors provide important conduits between areas of habitat (Beier 1993). Loss of population fragments in isolated habitat patches has also been shown (Beier 1993), demonstrating that habitat fragmentation can have negative consequences for animal populations. Tull and Krausman (2001) tracked mule deer *Odocoileus hemionus eremicus* and found that deer used a wildlife corridor as well as other routes to cross a canal. Movement corridors also increase movement in jumping spiders, showing that movement corridors may also be beneficial for invertebrate species (Baker 2007).

1.4 Between-patch movement, an aquatic perspective

Bowne and Bowers (2003) reviewed research on movement between habitat patches for 89 species, none of which were fish. The lack of knowledge on between-patch movement in fish is surprising, given the numerous studies on predation and complex habitat listed above. These studies indicate that complex habitat may provide benefits for aquatic species that parallel those for terrestrial ones. It is therefore reasonable to expect that movement between patches of complex habitat across open areas would pose similar risks for aquatic and terrestrial species, such as exposure to predators. Despite the lack of dedicated studies on between-patch movements in fishes, several studies have examined related behaviours in aquatic species.

The decision to choose a particular habitat patch has been studied in aquatic systems, focusing on the roles of foraging success and predation risk. Juvenile black surfperch *Embiotica jacksoni* select patches based on food quality, but physical structure becomes significant when predation risk is high (Schmitt and Holbrook 1985). Juvenile bluegill sunfish *Lepomis macrochirus* presented with patches of varying physical complexity, resource distribution, and predation risk chose patches that minimized the ratio of predation risk to foraging success (Gotceitas 1990). Another study of bluegill patch selection provided sunfish with patches of artificial vegetation and showed that bluegills select high-density habitat over low-density habitat as a refuge from predators (Gotceitas and Colgan 1987). Abrahams and Dill (1989) examined patch choice in guppies *Poecilia reticulata*, and found that predation risk could be quantified energetically by increasing food in a predator patch until equal numbers of fish fed at both a predator patch and a non-predator patch. Trade-

offs between foraging and predator evasion were further explored by Thistle (2006), who demonstrated that juvenile Atlantic cod densities were highest in eelgrass patches with intermediate fragmentation. Thistle (2006) suggested that this intermediate maximum represented a trade-off between use of eelgrass as a predator refuge while retaining access to more open areas for foraging.

In studies of patch departure decisions and residence times, also in bluegill sunfish, Marschall et al. (1989) presented sunfish with patches of artificial vegetation with either equal numbers of prey in each patch or different numbers of prey in each patch. They found that sunfish appeared to use a "constant residency" rule (an animal remains in a given patch for a "constant optimal amount of time"; Marschall et al. 1989). In contrast, DeVries et al. (1989) examined patch departure decisions by sunfish exposed to patches with the same number of prey at either high prey densities or low prey densities. Sunfish spent longer amounts of time in patches than predicted by a model of "giving up time", indicating that patch departure decisions for sunfish appear to be based on capture rate of prey (DeVries et al. 1989). These studies provide conflicting evidence on patch departure choices, but demonstrate that previous studies on between-habitat patch movement decisions in the aquatic environment examined the phenomenon from the perspective of foraging rules.

Research using artificial seagrass patches can also shed light on movement behaviour between suitable habitats by fish species. Sogard (1989) conducted colonization experiments to examine the effects of distance from a colonizing source on the community composition of a newly colonized patch. Fish and decapod crustaceans moved over open areas of bare substrate to reach patches of artificial

eelgrass, with different community composition in patches further from natural eelgrass than in those closer to colonizing sources (Sogard 1989). Further studies of migration into artificial eelgrass patches showed diel variation in immigration for some species of fish and decapod crustaceans (Sogard and Able 1994). Following addition of artificial eelgrass patches to sites with bare substrate, juvenile cod both settled and moved into the patches from surrounding areas (Laurel et al. 2003a). All of these studies with artificial eelgrass indicate that aquatic species move outside of complex habitat, but they do not identify the full extent of the movement, nor the factors that affect decisions to complete such migrations out of protective habitat.

As in terrestrial species, studies have examined the potential benefits of movement corridors for aquatic species. In estuarine systems, habitat corridors enhance the movement of several species, especially slow-moving macrofauna (Darcy and Eggleston 2005). Movement between stream pools was enhanced in some species of fish when movement corridors of complex overhead cover were created between the pools (Roberts and Angermeier 2007).

Overall, while many components of patch choice and departure have been studied in aquatic ecosystems, factors that affect between-patch movements have not been identified. Additionally, given the potential implications of between-patch movements for aquatic species, elucidating factors that affect such movement will improve our ability to manage ecosystems effectively. My research identifies factors that may affect between-patch movement in the cold-water demersal species Atlantic cod *Gadus morhua*. Greenland cod *Gadus ogac* were also used in two field experiments, though to a lesser extent, and those data are also included.

1.5 Study system

Atlantic cod are a demersal marine species of gadid fishes that inhabit the continental shelf of the northern Atlantic Ocean, from the coast of North Carolina in the western Atlantic, to the Bay of Biscay in the eastern Atlantic (Scott and Scott 1988). Atlantic cod spawn offshore in the late spring, resulting in buoyant fertilized eggs that float in the water column (Scott and Scott 1988). Fertilized eggs hatch into pelagic larvae, which settle into inshore coastal habitats or onto offshore banks at a length of approximately 25-50 mm (Lough and Bolz 1989, Methven and Bajdik 1994). The pelagic larvae settle into coastal areas in distinct pulses and then adopt a demersal lifestyle (Methven and Bajdik 1994, Ings et al. in press). Juvenile cod along the northeast coast of Newfoundland preferentially associate with beds of eelgrass, *Zostera marina* (Gotceitas et al. 1997, Laurel et al. 2003a, Laurel et al. 2004). The association with eelgrass and other complex habitat appears to be driven by predation risk, in that studies have shown reduced predation inside patches of eelgrass compared to eelgrass edges or open areas (Linehan et al. 2001, Laurel et al. 2003b). Previous work has shown that Atlantic cod will utilize preferred eelgrass habitat until population densities reach a maximum and "surplus" fish are relegated to sub-optimal fragments or open areas (Laurel et al. 2004).

Greenland cod are demersal marine fish that inhabit coastal areas of the Arctic Ocean and northwest Atlantic Ocean from Alaska to Greenland and south to Nova Scotia (Scott and Scott 1988). Greenland cod spawn in the nearshore and have a demersal egg stage, in contrast to the pelagic eggs of Atlantic cod (Scott and Scott 1988). Greenland cod appear to be highly site specific during the juvenile stage

(Mikhail and Welch 1989), and remain in nearshore areas for the duration of their life (Mikhail and Welch 1989, Sheppard 2005).

Eelgrass is a wide-ranging species of seagrass that occurs throughout the northern Pacific and Atlantic oceans, predominantly in the sub-tidal zone (den Hartog 1971, Duarte 1991). Eelgrass may reproduce either sexually or vegetatively, although dispersal is believed to be primarily through vegetative reproduction (den Hartog 1971). This pattern of reproduction results in a naturally fragmented distribution, with eelgrass growing in patterns ranging from contiguous meadows to sparse patches in large, open areas (Robbins and Bell 1994). The natural growth pattern of eelgrass and the association of juvenile cod with eelgrass habitat create a natural system for studies of between-patch movement. Juvenile Atlantic cod experience a range of habitat patchiness, and may be regularly subject to changing conditions that necessitate their movement between habitat patches.

While there is evidence that juvenile cod in contiguous eelgrass exhibit low site fidelity and move in ways that do not correspond to movement models of simple diffusion (Laurel et al. 2004), there are multiple studies that suggest high site fidelity in juvenile cod. Grant and Brown (1998) and Sheppard (2005) found high site fidelity and movement at scales limited to only a few hundred meters in contiguous eelgrass. Tupper and Boutilier (1995) suggested that post-settled cod in Nova Scotia were highly site specific and exhibited territoriality. These studies on juvenile cod in continuous eelgrass suggest that there may be variation in movement patterns, but do not address the potential effects of gaps that are commonly part of eelgrass habitat. By examining the effects of gaps in eelgrass habitat on movement behaviour on

juvenile cod, I add to the literature on juvenile cod movement and expand the applicability of gap-dynamics studies that, until now, have focused mainly on terrestrial systems.

1.6 References

Abrahams, M.V., Dill, L.M. 1989. A determination of the energetic equivalence of the risk of predation. Ecology 70: 999-1007.

Andreassen, H.P., Ims, R.A., Steinset, O.K. 1996. Discontinuous habitat corridors: effects on male root vole movements. Journal of Applied Ecology 33: 555-560.

Andrén, H. 1994. Effects of habitat fragmentation on birds and mammals in landscapes with different proportions of suitable habitat: a review. Oikos 71: 355-366.

Baker, L. 2007. Effects of corridors on the jumping behaviour of the jumping spider *Phidippus princeps* (Araneae, Salticidae). Canadian Journal of Zoology 85: 802-808.

Beier, P. 1993. Determining minimum habitat area and habitat corridors for cougars. Conservation Biology 7: 94-108.

Beier, P., Noss R.F. 1998. Do habitat corridors provide connectivity? Conservation Biology 12: 1241-1252.

Bélisle, M., Desrochers, A. 2002. Gap-crossing decisions by forest birds: an empirical basis for parameterizing spatially-explicit, individual-based models. Landscape Ecology 17: 219-231.

Bosschieter, L., Goedhart, P.W. 2005. Gap crossing decisions by reed warblers (*Acrocephalus scirpaceus*) in agricultural landscapes. Landscape Ecology 20: 455-468.

Bowman, J., Fahrig, L. 2002. Gap crossing by chipmunks: an experimental test of landscape connectivity. Canadian Journal of Zoology 80: 1556-1561.

Bowne, D.R., Bowers, M.A. 2004. Interpatch movements in spatially structured populations: a literature review. Landscape Ecology 19: 1-20.

Bright, P.W. 1998. Behaviour of specialist species in habitat corridors: arboreal dormice avoid corridor gaps. Animal Behaviour 58: 1485-1490.

Cassini, M.H. 1991. Foraging under predation risk in the wild guinea pig *Cavia aperea*. Oikos 62: 20-24.

Creegan, H.P., Osborne, P.E. 2005. Gap-crossing decisions of woodland songbirds in Scotland: an experimental approach. Journal of Applied Ecology 42: 678-687.

Darcy, M.C., Eggleston, D.B. 2005. Do habitat corridors influence animal dispersal and colonization in estuarine systems? Landscape Ecology 20: 841-855.

den Hartog, C. 1971. The dynamic aspect in the ecology of seagrass communities. Thalassi Jugosl 7: 101-112.

Desrochers, A., Hannon, S. J. 1997. Gap crossing decisions by forest songbirds during the post-fledgling period. Conservation Biology 11: 1204-1210.

DeVries, D.R., Stein, R.A., Chesson, P.L. 1989. Sunfish foraging among patches: The patch-departure decision. Animal Behaviour 37: 455-464.

Duarte, C.M. 1991. Seagrass depth limits. Aquatic Botany 40: 363-377.

Frid, A. 1997. Vigilance by female Dall's sheep: interactions between predation risk factors. Animal Behavior 53: 799-808.

Gilliam, J.F., Fraser, D.F. 2001. Movement in corridors: enhancement by predation threat, disturbance and habitat structure. Ecology 82: 258-273.

Gotceitas, V. 1990. Foraging and predator avoidance: a test of a patch choice model with juvenile bluegill sunfish. Oecologia 83: 346-351.

Gotceitas, V., Fraser, S., Brown, J.A. 1997. Use of eelgrass beds (*Zostera marina*) by juvenile Atlantic cod (*Gadus morhua*). Canadian Journal of Fisheries and Aquatic Sciences 54: 1306-1319.

Gotceitas, V., Colgan, P. 1987. Selection between densities of artificial vegetation by young bluegills avoiding predation. Transactions of the American Fisheries Society 116: 40-49.

Gotceitas, V., Colgan, P. 1989. Predator foraging success and habitat complexity: quantitative test of the threshold hypothesis. Oecologia, 80: 158-166.

Grant, S.M., Brown, J.A. 1998. Nearshore settlement and localized populations of age-0 Atlantic cod (*Gadus morhua*) in shallow coastal waters of Newfoundland. Canadian Journal of Fisheries and Aquatic Sciences 55: 1317-1327.

Graves T.A., Farley, S., Goldstein, M.I., Servheen, C. 2007. Identification of functional corridors with movement characteristics of brown bears on the Kenai Peninsula, Alaska. Landscape Ecology 22: 765-772.

Grubb Jr., T.C., Doherty Jr., P.F. 1999. On home-range gap-crossing. The Auk 116: 618-628.

Hogstad, O. 1986. Social rank and antipredator behaviour of willow tits *Parus montanus* in winter flocks. Ibis 130: 45-56.

Ings, D.W., R.S. Gregory, D.C. Schneider. In press. Episodic downwelling predicts recruitment of Atlantic cod, Greenland cod and white hake to Newfoundland coastal waters. Journal of Marine Research. 66: 000-000.

Kie, J.G., Ager, A.A., Bowyer, R.T. 2005. Landscape-level movements of North American elk (*Cervus elaphus*): effects of habitat patch structure and topography. Landscape Ecology 20: 289-300.

Kopp, K., Wachlevski, M., Eterovick, P.C. 2006. Environmental complexity reduces tadpole predation by water bugs. Canadian Journal of Zoology 84: 136-140.

Kotler, B.P. 1984. Risk of predation and the structure of desert rodent communities. Ecology 65: 689-701.

Laurel, B.J., Gregory, R.S., Brown, J.A. 2003 (a). Settlement and distribution of Age-0 juvenile cod, *Gadus morhua* and *G. ogac*, following a large-scale habitat manipulation. Marine Ecology Progress Series 262: 241-252.

Laurel, B.J., Gregory, R. S., Brown, J.A. 2003 (b). Predator distribution and habitat patch area determine predation rates on age-0 Atlantic cod, *Gadus* spp. Marine Ecology Progress Series 251: 245-254.

Laurel, B.J., Gregory, R.S., Brown, J.A., Hancock, J.K., Schneider, D.C. 2004. behavioural consequences of density-dependent habitat use in juvenile Atlantic cod *Gadus morhua* and *G. ogac*: the role of movement and aggregation. Marine Ecology Progress Series 272: 257-270.

Lima, S.L. 1990. Protective cover and the use of space: different strategies in finches. Oikos 58: 151-158.

Lima, S.L., Dill, L.M. 1990. Behavioural decisions made under the risk of predation: a review and prospectus. Canadian Journal of Zoology 68: 619-640.

Lima, S.L., Wiebe, K.L., Dill, L.M. 1987. Protective cover and the use of space by finches; is closer better? Oikos 50: 225-230.

Linehan, J.E., Gregory, R.S., Schneider, D.C. 2001. Predation risk of age-0 cod (*Gadus*) relative to depth and substrate in coastal waters. Journal of Experimental Marine Biology and Ecology 263: 25-44.

Lough, R.G, Bolz, G.R. 1989. The movement of cod and haddock larvae onto the shoals of Georges Bank. Journal of Fish Biology 35(Supplement A): 71-79.

Magurran, A.E., Irving, P.W., Henderson, P.A. 1996. Is there a fish alarm pheromone? A wild study and critique. Proceeding of the Royal Society of London B 263: 1551-1556.

Marschall, E.A., Chesson, P.L., Stein, R.A. 1989. Foraging in a patchy environment: prey-encounter rate and residence time distributions. Animal Behaviour 37: 444-454.

Martella, M.B., Renison, D., Navarro, J.L. 1995. Vigilance in the greater rhea: effects of vegetation height and group size. Journal of Field Ornithology 66: 215-220.

Methven, D.A., Bajdik, C. 1994. Temporal variation in size and abundance of juvenile Atlantic cod (*Gadus morhua*) at an inshore site off eastern Newfoundland. Canadian Journal of Fisheries and Aquatic Sciences 51: 78-90.

Mikhail, M.Y., H.E. Welch. 1989. Biology of Greenland cod, Gadus ogac, at Saqvaqjuac, northwest coast of Hudson Bay. Environmental Biology of Fishes, 26: 49-62.

Newman, J.A., Recer, G.M., Zwicker, S.M., Caraco, T. 1988. Effects of predation hazard on foraging "constraints": patch use strategies in grey squirrels. Oikos 53: 93-97.

Norris, D.R., Stutchbury, B.J.M. 2002. Sexual difference in gap-crossing ability of a forest songbird in a fragmented landscape revealed through radiotracking. The Auk 119: 528-532.

Roberts, J.H., Angermeier, P.L. 2007. Movement responses of stream fishes to introduced corridors of complex cover. Transactions of the American Fisheries Society 136: 971-978.

Robbins, B.D., Bell, S.S. 1994. Seagrass landscapes; a terrestrial approach to the marine subtidal environment. Trends in Ecology and Evolution 9: 301-304.

Rood, J.P. 1972. Ecological and behavioural comparisons of three genera of Argentina cavies. Animal Behaviour Monographs 5: 1-83.

Ruefenacht, B., Knight, R.L. 1995. Influences of corridor continuity and width on survival and movement of deermice. Biological Conservation 71: 269-274.

Savino, J.F.,Stein, R.A. 1982. Predator-prey interactions between largemouth bass and bluegills as influenced by simulated submersed vegetation. Transaction of the American Fisheries Society 11: 255-266.

Schmitt, R.J., Holbrook, S.J. 1985. Patch selection by juvenile black surfperch (Embiotocidae) under variable risk: Interactive influence of food quality and structural complexity. Journal of Experimental Marine Biology and Ecology 85: 269-285.

Schneider, K.J. 1984. Dominance, predation and optimal foraging in white-throated sparrow flocks. Ecology 65: 1820-1827.

Scott, W.B., Scott, M.G. 1988. Atlantic Fishes of Canada. Canadian Bulletin of Fisheies and Aquatic Sciences 219: 713 pp.

Sheppard, G.L. 2005. Natural mortality and movement of juvenile cod (*Gadus* spp.) inhabiting eelgrass (*Zostera marina*) in coastal Newfoundland waters. MSc Thesis, Department of Biology, Memorial University of Newfoundland.

Smith, R.J. 1997. Does one result trump all others? A response to Magurran, Irving and Henderson. Proceedings of the Royal Society of London B 264: 445-450.

Sogard, S.M. 1989. Colonization of artificial seagrass by fishes and decapod crustaceans: importance of proximity to natural eelgrass. Journal of Experimental Marine Biology and Ecology 133: 15-37.

Sogard, S.M., Able, K.W. 1994. Diel variation in immigration of fishes and decapod crustaceans to artificial seagrass habitat. Estuaries 17(3): 622-630.

Sogard, S.M., Olla, B.L. 1993. The influence of predator presence on utilization of artificial seagrass habitat by juvenile walleye pollock, *Theragra chalcogrammu.* Environmental Biology of Fishes 37: 57-65.

Thistle, M. E. 2006. Distribution and risk-sensitive foraging of juvenile gadids in relation to fractal complexity of eelgrass (*Zostera marina*) habitat. MSc Thesis. Memorial University of Newfoundland, St. John's, NL.

Tischendorf, L., Wissel, C. 1997. Corridors as conduits for small animals; attainable distance depending on movement. Oikos 79: 603-611.

Tull, J.C., Krausman, P.R. 2001. Use of a wildlife corridor by mule deer. The Southwestern Naturalist 46: 81-86.

Tupper, M., Boutilier, R.G. 1995. Effects of habitat on settlement, growth and postsettlement survival of Atlantic cod (*Gadus morhua*). Canadian Journal of Fisheries and Aquatic Sciences 52: 1834-1841.

Tupper, M., Boutilier, R.G. 1997. Effects of habitat on settlement, growth, predation risk and survival of a temperature reef fish. Marine Ecology Progress Series 151: 225-236.

Wywialowski, A.P. 1987. Habitat structure and predators: choices and consequences for rodent habitat specialists and generalists. Oecologia 72: 39-45.

Zollner, P.A., Lima, S.L. 1999. Illumination and the perception of remote habitat patches by white-footed mice. Animal Behaviour 58: 489-500.

Co-authorship statement

Chapter 2: Between-patch movement of juvenile Atlantic cod (*Gadus morhua*)

Mary R. Ryan designed the research program, collected all data, analyzed all data, and prepared the manuscript. Robert S. Gregory contributed ideas, advised on experimental design, and contributed to manuscript editing. Paul V.R.. Snelgrove contributed ideas, advised on statistical analyses and contributed to manuscript editing. Shaun S. Killen advised on experimental design, assisted with data collection, and contributed to manuscript editing. Danny W. Ings advised on statistical analyses.

Chapter 3: Description of inter-patch movement by juvenile cod (*Gadus* spp.) in a coastal Newfoundland fjord: a mark-recapture study

Mary R. Ryan designed the research program, organized collection of all data, analyzed all data, and prepared the manuscript. Robert S. Gregory contributed ideas, advised on experimental design, advised on the field research, assisted in data collection, advised on statistical analysis, and assisted with manuscript editing. Paul V.R.. Snelgrove contributed ideas, advised on experimental design, advised on statistical analysis, and contributed to manuscript editing. Danny W. Ings advised on statistical analyses.

Chapter 2: Between-patch movement of juvenile Atlantic cod (*Gadus morhua*)

2.1 Introduction

Variation in the complexity of habitat modifies predation risk for a variety of animals and, in doing so, drives many components of animal behaviour. Physically complex habitat may inhibit the ability of an animal to detect a predator (Martella et al. 1995, Frid 1997). Conversely, complex habitat may decrease predation rate or reduce the efficiency of predators, thereby providing refuge for prey organisms (Lima and Dill 1990, Pierce et al. 2004). Reduction in predation rates may result from a decrease in the ability of predators to detect prey when in complex habitat (Crowder and Cooper 1982, Kopp et al. 2006), or a shift in predation tactics when in physically complex areas (Savino and Stein 1982). Behaviours that minimize the potential risk of moving outside areas of complex habitat have been observed in terrestrial species including forest songbirds (Desrochers and Hannon 1997, Bélisle and Desrochers 2002, Creegan and Osborne 2005), reed warblers *Acrocephalus scirpaceus* in agricultural landscapes (Bosschieter and Goedhart 2005), and white-footed mice *Peromyscus leucopus* (Zollner and Lima, 1999). The avoidance of movement outside of physically complex habitat by many species has led to a large body of research on terrestrial movement corridors (see Beier 1993, Tull and Krausman 2001, Baker 2007). To date, however, little work has focused on similar phenomena in marine habitats.

Several studies have documented the capacity of physically complex habitat to reduce predation risk for marine species (Savino and Stein 1982, Sogard and Olla 1993, Linehan et al. 2001). This attribute would suggest that the avoidance of open

areas demonstrated for terrestrial species may also occur in marine fauna. Patch departure studies on foraging bluegill sunfish *Lepomis macrochiru* indicate that foraging success may affect the amount of time before an animal seeks a new resource patch (DeVries et al. 1989, Gotceitas 1990), while related studies on surfperch have shown that predator presence interacts with foraging factors to affect patch departure decisions (Schmitt and Holbrook 1985). Colonization studies such as those conducted by Sogard (1989) show that different species of fish and decapod crustaceans vary in their willingness to move over open areas, or that different species may move at different speeds over open areas. However, no published studies have focused specifically on the movement of fish after leaving a patch of complex habitat, or the factors that affect behaviour during such movement.

In this study, I examined the between-patch movements of juvenile Atlantic cod *Gadus morhua*, a potential model species for between-patch movement in marine environments. Atlantic cod distributions in the western Atlantic Ocean range from Greenland in the north to Cape Hatteras in North Carolina in the south (Scott and Scott 1988). Juvenile Atlantic cod inhabit bays (Methven and Bajdik 1994) or offshore banks (Lough and Bolz 1989) in demersal habitats following a pelagic larval stage. In bays along the northeast coast of Newfoundland, numerous studies have demonstrated an association between juvenile cod and complex habitat such as cobble or eelgrass *Zostera marina* (Gotceitas et al. 1997, Grant and Brown 1998, Laurel et al. 2003a, Laurel et al. 2003b). Linehan et al. (2001) demonstrated that eelgrass habitat significantly reduces predation on juvenile Atlantic cod by cunner *Tautogolaubrus adspersus*, larger Atlantic cod, and Greenland cod, *G. ogac*. Laurel et

al. (2003b) further demonstrated that juvenile cod experience lower predation rates in larger eelgrass patches as compared to smaller patches, but the benefit of increasing patch size may be diminished at very large patch sizes as a result of increased predator density. This work illustrates the potential benefit of eelgrass to juvenile cod and the increased risk to juveniles of departure from eelgrass patches. This increased risk is corroborated by work showing high degrees of aggregation by juvenile cod in areas outside of complex habitat (Laurel et al. 2004). Grouping behaviour has been shown to be a response to predation risk in multiple marine and terrestrial species (Pitcher 1986, Wrona and Jamieson Dixon 1991, Cresswell 1994, Lingle 2001).

Previous work on Atlantic cod has yielded highly variable results regarding scales of movement, with some studies showing that movement is restricted to scales of hundreds of metres (Tupper and Boutilier 1995, Grant and Brown 1998, Sheppard 2005), and others suggesting much higher levels (Laurel et al. 2004). None of these studies have examined movement between patches of complex habitat, and none have identified the factors that affect movement behaviour. This work represents the first study of juvenile fish behaviour that identifies the mechanisms that affect between-patch movement. Specifically, this study addressed the effects of different initial fish densities in a patch, different between-patch distances, and how the presence of a predator near patches affects between-patch movement behaviour of juvenile Atlantic cod. I hypothesized that greater initial fish densities in a patch would decrease the amount of time before fish initially departed a release patch and increase the number of times the fish moved between patches. For the distance trials, I expected that an increased between-patch distance would result in a longer time before initial

departure from the release patch, fewer between-patch movements, and faster between-patch movements. Finally, for the predator trial, I expected that the presence of a predator would increase the length of time before initial departure from the patch into which the fish were released, decrease the number of between-patch movements and increase the speed of between patch movements. For all experiments, I expected that larger fish would depart the release patch earlier, complete more between-patch movements, and move faster between patches.

2.2 Methods

2.2.1 Study species

Approximately 500 juvenile Atlantic cod were captured in Smith Sound, Trinity Bay (see Figure 2.1) in July 2007 using a beach seine, and then transferred to the Ocean Sciences Centre, Logy Bay in seawater containing airstones for aeration. At the Ocean Sciences Centre, fish were held in flow-through ambient seawater holding tanks (1.0 m x 1.0 m x 0.5 m; approximately 150 fish per tank) and fed chopped herring *Clupea harengus* daily to satiation. Water temperature fluctuated between 1 °C and 15 °C over the course of the study period because of local hydrographic events; however, no experiments were conducted when temperatures dropped below 8 °C. During density and distance trials, I controlled photoperiod with timers in order to mimic natural diel timing for the appropriate latitude (approximately 16h light: 8h dark during the study period). Predator experiments were completed in the fall, when natural day length was shorter than during the summer. In order to ensure that all experiments were conducted with fish that had

experienced similar photoperiods, for the predator experiments I followed a fixed 16h light: 8h dark photoperiod schedule. All fish were fasted for 24 hrs prior to exposure to experimental conditions.

An age 3+ wild caught Atlantic cod (*Gadus morhua*, 43 cm, standard length) that had been held at the Ocean Sciences Centre for approximately three years was used as the predator for the predator experiments. Though a predator held in captivity might arguably represent a less efficient predator than one recently obtained from the wild, my objective was to create a visual cue to the juvenile fish rather than test actual predation rates or efficiency. One week prior to beginning experiments, the predator fish was transferred into a holding tank (1.0 m x 1.0 m x 0.5 m) supplied with ambient seawater and with airstones for aeration (water temperature in the predator holding tank fluctuated between 1 °C and 10 °C over the course of the experiments). The predator was fed dry pellets on Mondays, Wednesdays and Fridays to satiation in accordance with the schedule previously established at the Ocean Sciences Centre.

2.2.2 Fish tagging

Prior to the first experiment, I lightly anaesthetized juvenile cod with 2-phenoxyethanol (0.30 ml/L) until equilibrium was lost (fish could no longer maintain upright orientation) and opercular movement was reduced. I used surgical suture to affix two coloured plastic beads (diameter = 2 mm) to each fish in the dorsal musculature anterior to the dorsal fin, after which the fish were placed in a large bucket of aerated seawater to recover. The tagging increased visibility in the experimental arena and differentiated the focal fish from other fish in the release groups.

Prior to the second experiment on between-patch distance effects, fish that had lost tags were re-anaesthetized as described above and new beads were attached. I repeated this procedure prior to the third and final set of experiments with predators, for fish that had lost tags and that had not already been subjected to a second bead surgery. All fish were given a minimum of three days to recover following any tagging surgery before being placed in the experimental arena. Over the course of the entire experimental period, tag loss occurred at a rate of approximately one percentt per day.

2.2.3 Experimental arena

I used a large flow-through 12 m x 3 m raceway supplied with ambient seawater and surrounded by a blind as the test arena for all experiments. The bottom of the tank was lined with small gravel (approximately 0.5 cm diameter), and the water depth was approximately 1.5 m. I marked one side of the tank with pieces of flagging tape to indicate the boundaries of numbered crosswise sections of the experimental arena (see Figures 2.2, 2.3 and 2.4). Lighting was provided by a series of overhead lights that created as uniform light coverage as possible and remained constant for all experimental trials. I constructed patches of artificial eelgrass by affixing green polypropylene ribbon (width = 4.7 mm, length = 75 cm) to a wire mesh base at a density of 700 stems per m^2 (method based on Laurel et al 2003a); I selected this density to fall within the range of natural eelgrass (Orth et al. 1984, Gotceitas et al. 1997). Previous studies have shown that artificial eelgrass adequately mimics natural eelgrass in lab and field habitat studies (e.g. Sogard and Olla 1993, Gotceitas et al. 1997, Laurel et al. 2003a). I arranged patches 2.5 m^2 in area in varying

configurations within the tank with the exact layout dependent on individual experiments and treatments. One patch served as the release location for all experiments and treatments and its location was constant throughout my experiments (see Figures 2.2, 2.3 and 2.4).

Fish were randomly removed from holding tanks prior to the start of each trial. I lowered fish into the release patch in a wire cage (50 cm x 40 cm x 15 cm) that was hinged on one side. After approximately 5 minutes, I opened the cage from outside the blind using a rope affixed to the hinged side. I made all observations through viewing slits cut in the blind and observed one randomly selected "focal animal" continually for the duration of the trial (durations varied depending on the experiment, see descriptions below). The trial began when the focal fish left the release cage, which was immediate for some individuals and up to 5 or 6 minutes for others. The section location of the focal fish was recorded continuously throughout the length of the trial, as was the number of individuals within any group that the focal fish joined. I considered fish to be part of a group if they were located within 3 body lengths of each other and moved in the same direction. Any attacks or startle behaviours were also noted. I considered the location of the fish to be on the edge of an eelgrass patch if the fish was within one body length of the outermost edge of the patch.

2.2.4 Experimental design: Release density

I divided the experimental arena into a 2.0 m release section, a 2.0 m destination section located at the opposite end of the experimental arena, and seven 1.1 m transit sections in between (Figure 2.2). This layout created a total distance of

approximately 8 m between the release and destination patches. I further divided the release and destination sections into eelgrass and non-eelgrass sections, with artificial eelgrass patches occupying all of each of these sections except for approximately 20 cm of non-eelgrass border. Additionally, the placement of the destination patch was identical in all trials and avoided the standpipe located at that end of the arena, although the standpipe appeared to have no effect on fish behaviour.

I tested release densities of 1, 5, or 10 fish in replicate trials in order to determine the effect of release density on between-patch movement. All fish were experimentally naïve to the test conditions (i.e. none were reused for multiple trials) and were selected at random from the holding tanks prior to each experiment. I released the fish into the experimental arena using the method described above and observed a randomly-selected focal fish for the duration of the trial. Mean fish length (± standard error) for this experiment was 103.9 ± 3.3 mm (standard length). Mean focal fish lengths (± standard error) for this experiment were 99.5 ± 31.5 mm, 99.8 ± 31.6 mm, and 114.2 ± 36.1 mm (standard length) for release densities of 1 fish, 5 fish, and 10 fish, respectively. All trials lasted 30 minutes and all observations were made using the PSION observation recorder (™Noldus Information Technology, Wageningen, The Netherlands). I selected a trial length of 30 minutes following two sets of preliminary observations lasting approximately one hour. During these preliminary trials, I noted that fish initially left the release patch early in the observation period and so I chose to observe all experimental subjects for 30 minutes to encompass the behaviours associated with early movements outside of protective

habitat. Each density (1 fish, 5 fish, and 10 fish) was replicated 10 times, resulting in a total of 300 minutes of observation for each of the release densities tested.

2.2.5 Experimental design: Between-patch distance

I divided the arena into seven 1.5 m sections, with a release patch in one end, and the destination patch placed either 3 m or 7.5 m away (see figure 2.3). Given the smaller section sizes for the release and destination patches (compared to 2 m sections used in the density experiment), the patches in these trials bordered the sections in which they were located. The change in section markers compared to the density experiment reflected the fact that, because I had moved the destination patch from the extreme end of the experimental arena to a closer location, section markers had to be moved to achieve the identical sections sizes that represented a more appropriate experimental design.

I released 5 fish at a time to test the effects of varying between-patch distances on between-patch movement. Groups of 5 fish were used in order to balance the need to allow the focal fish to associate with conspecifics while still allowing me to easily determine the number of fish in any given group. All fish were experimentally naïve to the test conditions and were selected at random from the holding tanks prior to each experiment. I released the fish into the arena using the method described above and observed a randomly-selected focal fish for the duration of the trial Mean fish length (± standard error) for this experiment was 110.7 ± 4.1 mm, standard length. Mean focal fish lengths (± standard error) for this experiment were 113.8 ± 3.6 mm and 110.1 ± 6.2 mm, (standard length) for between-patch distances of 3 m and 7.5 m, respectively. Following preliminary analysis of the release density experiment, I

determined that fish generally left the release patch within 2-3 minutes of release and completed between-patch movements within 5-10 minutes of release (if they completed between-patch movements at all). I therefore decided to reduce the observation time to 15 minutes for both this experiment and the subsequent predator experiment because the behaviour of interest was exhibited within 15 minutes of release. All trials lasted 15 minutes and all observations were made using the PSION observation recorder described above. I tested each distance with 10 separate groups of fish, resulting in 150 minutes of observation for each distance tested.

2.2.6 Experimental design: Predator presence

I constructed a predator enclosure using a 56 L plastic container, from which I removed the side panels and replaced them with fine wire mesh (mesh opening = 2 mm). This modification resulted in an enclosure that allowed transmission of any visual and chemical cues from the predator to experimental subjects. The predator was placed into the enclosure and the enclosure placed in the experimental arena prior to fish release.

I divided the arena into seven 1.5 m sections with the release patch at one end of the experimental arena and the destination patch positioned 7.5 m away (see Figure 2.4). I tested two predator locations; one approximately 0.5 m from the outermost edge of the release patch (predator location 1) and the other approximately 0.5 m from the edge of the destination patch closest to the release patch (predator location 2; see Figure 2.4).

I released 5 fish at a time to test the effects of predator presence on between-patch movement. As in the between-patch distance experiment, groups of 5 fish were

used in order to allow the focal fish to associate with conspecifics while still allowing me to easily determine the number of fish in any given group. All fish were experimentally naïve to the test conditions and were selected at random from the holding tanks prior to each experiment. I released fish into the arena using the method described above and observed a randomly-selected focal fish for the duration of the trial. Mean fish length (± standard error) for this experiment was 138.8 ± 4.8 mm, standard length. Mean focal fish lengths (± standard error) for this experiment were 141.8 ± 44.8 mm and 133.7 ± 42.3 mm, (standard length) for enclosure locations beside the release patch and destination patch, respectively. All trials lasted 15 minutes and all observations were made using the PSION observation recorder described above. Each group of fish was released twice into the experimental arena. During the first release, I observed the fish in the presence of an empty predator enclosure. I then removed the fish from the arena, and after approximately 20 minutes, re-released them into the arena for a second set of observations. During the second release, I observed the fish in the presence of the enclosure at the same location as the first observations, but now containing the predator. I recorded the behaviour of the same focal animal during both observational periods. This strategy controlled for the presence of the enclosure, and allowed me to observe the behaviour of the same fish before and during predator exposure. I tested each predator location and the corresponding enclosure control with 10 groups of fish, resulting in 150 minutes of observation for each predator and control location tested.

2.2.7 Data analysis

For each focal fish observed, I recorded the total number of between-patch movements and the amount of time taken to complete each movement. I then calculated the average duration of between-patch movements for each focal fish and used this value in subsequent analyses. Similarly, I calculated an average group size for each focal animal by summing the amount of time spent in each possible group size and determining the weighted average. I analyzed all data using the proc GENMOD in SAS (Release 9.1). The GENMOD procedure inputs data into a general linear model and calculates p-values for the model in question based on maximum likelihood. I have provided an example of a full model and the results from the GENMOD procedure in Appendix 1. All figures were created in SigmaPlot based on results from the GENMOD procedure. For each experiment, I constructed models examining the variable of average group size as dependent on the experimental conditions, and separate models including it as a potential explanatory variable. I used this approach because while many species have been shown to aggregate as a defense mechanism (Cresswell 1994, Foster and Treherne 1981, Krebs and Davies 1991), how the presence of conspecifics affects movement between patches of habitat is unknown. I included all explanatory variables (group size, fish length, and experimental variable) in a model to test the significance of their interaction on each of the response variables of interest (time before the focal fish departed the release patch, average duration or speed of completed between-patch movements, and total number of completed between-patch movements). If no three-way interactions were present, pairs of explanatory variables, and then individual explanatory variables were

tested separately to evaluate effects of individual variables. If a three-way interaction was present and one of the variables was a class variable, I isolated each of the classes and tested the remaining two variables for significant interactions. The results of these tests are noted below. I evaluated model significance using p-values, and examined all residuals for normality, randomness, independence, and homogeneity where appropriate. When the data were not normal, I used a gamma or poisson distribution. Average duration of between-patch movements was used in the predator and density experiments, whereas I calculated average between-patch movement speed for the distance trials. This approach corrected for the difference in distance travelled by the fish, however, it should be noted that average speed does not represent an actual swim speed (i.e. body lengths per second) but rather the total between-patch distance divided by the total time taken to move between patches. I recorded standard errors for all mean values and report them below.

2.3 Results

2.3.1 Release density experiment

Fish released with higher numbers of conspecifics were observed in larger average groups ($\chi^2 = 34.04$; df = 2, n =30, $p < 0.0001$). Fish released alone had no opportunity to associate with conspecifics, while fish released with four others formed groups with a mean size of 2.41 ± 0.76 and fish released with ten others formed groups with a mean size of 4.46 ± 1.41. There was no effect of fish length on group size ($\chi^2 = 1.26$; df = 1, n =29, $p = 0.2619$).

The length of time before focal fish first departed the release patch was significantly affected by the interaction of release density and group size ($\chi^2 = 9.62$; df = 1, n = 30, p = 0.0019). At a release density of 1 fish, mean release patch departure time was 56.11 ± 17.74 seconds. At a release density of 5, fish in larger groups took significantly longer to depart from the release patch than fish in smaller groups ($\chi^2 = 9.19$; df = 1, n = 10, p = 0.0024; Figure 2.5); at a release density of 10 fish, there was no effect of group size on initial departure time from the release patch ($\chi^2 = 0.53$; df = 1, n = 10, p = 0.4654; Figure 2.5). Fish length had no effect on the initial departure time from the release patch ($\chi^2 = 2.01$; df = 1, n = 29, p = 0.1563).

Larger fish moved between patches more quickly than smaller fish ($\chi^2 = 10.22$; df = 1, n = 26, p = 0.0014; Figure 2.6). Neither group size nor release density had significant effects on the duration of between-patch movements ($\chi^2 = 1.75$; df = 2, n = 26, p = 0.4172 and $\chi^2 = 1.03$; df = 1, n = 26, p = 0.3108 for release density and group size, respectively). Moreover, there were no significant interactive effects on duration of between-patch movements for any of the variables tested.

The total number of between-patch movements was unaffected by release density ($\chi^2 = 0.62$; df = 2, n = 30, p = 0.7349), but was significantly affected by the interaction of group size and fish length ($\chi^2 = 7.16$; df = 1, n = 30, p = 0.0075). These results were unexpected given the highly significant effect of release density on group size, which likely resulted from release density limiting potential group size.

2.3.2 Between-patch distance experiment

There was no difference in average group size for fish exposed to different between-patch distances ($\chi^2 = 0.48$; df = 1, n = 20, p = 0.4892), nor was there any effect of fish length on average group size ($\chi^2 = 1.53$; df = 1, n = 20, p = 0.2157).

The length of time before focal fish initially departed the release patch was significantly affected by a three-way interaction among between-patch distance, fish length, and group size ($\chi^2 = 6.18$; df = 1, n = 20, p = 0.0129).

The effect of between-patch distance on average movement speed was not significant at the 0.05 level, but was significant at the 0.10 level ($\chi^2 = 3.61$; df = 1, n = 18, p = 0.0576). Fish moved an average of 0.12 ± 0.01 m/s (mean ± SE) and 0.16 ± 0.02 m/s when exposed to between patch distances of 3 m and 7.5 m, respectively. Movement speed was also significantly affected by the interaction of length and group size ($\chi^2 = 4.22$; df = 1, n = 18, p = 0.0400).

The total number of between patch movements decreased significantly at the longest distance tested ($\chi^2 = 3.89$; df = 1, n = 20, p = 0.0487). Focal fish exposed to a 3 m between-patch distance moved between patches an average of 4.6 ± 0.6 times whereas fish exposed to a 7.5 m between-patch distance moved between patches an average of only 2.9 ± 0.7 times. Group size had a positive effect on the total number of between-patch movements, however, this relationship was only significant at the 0.10 level ($\chi^2 = 3.72$; df = 1, n = 20, p = 0.0537; Figure 2.7). Fish length had no effect on the total number of between-patch movements ($\chi^2 = 0.20$; df = 1, n = 20, p = 0.6576).

2.3.3 Predator experiment

There was no difference in average group size for fish exposed to different predator conditions ($\chi^2 = 7.00$; df = 3, n = 40, p = 0.0720), nor was there any effect of length on average group size ($\chi^2 = 2.38$; df = 1, n = 38, p = 0.1238).

The time taken to initially depart the release patch was significantly affected by a three-way interaction between the predator variable (presence and location), group size, and fish length ($\chi^2 = 20.17$; df = 3, n = 36, p = 0.0002). I further explored this interaction by comparing pairs of predator treatments to determine if the three-way interaction remained significant. This three-way interaction was significant when comparing the presence of the predator at the edge of the release patch to the control at the edge of the release patch ($\chi^2 = 8.59$; df = 1, n = 18, p = 0.0034), as well as the presence of the predator at the edge of the destination patch to the control at the edge of the destination patch ($\chi^2 = 10.33$; df = 1, n = 18, p = 0.0013). The interaction of these three factors was also significant when comparing the presence of the predator at each of the two locations tested ($\chi^2 = 7.35$; df = 1, n = 17, p = 0.0067).

The average duration of completed between-patch movements in the predator experiment was significantly affected by the interaction between the predator variable and group size ($\chi^2 = 12.35$; df = 3, n =27, p = 0.0063). Fish in smaller groups moved more slowly between patches when the predator was located at the edge of the release patch ($\chi^2 = 4.50$; df = 1, n = 6, p = 0.0339), however there was no effect of group size when fish were presented with the empty enclosure at the same location ($\chi^2 = 0.73$; df = 1, n = 7, p = 0.3932; Figure 2.8). When the predator was located at the edge of the destination patch, group size had no effect on the duration of between-patch

movements ($\chi^2 = 2.62$; df = 1, n = 6, p = 0.1056); however, when fish were presented with an empty enclosure at the same location, fish in smaller groups moved more quickly between patches ($\chi^2 = 6.36$; df = 1, n = 6, p = 0.0117; Figure 2.9).

The total number of between-patch movements was significantly affected by the overall predator variable ($\chi^2 = 15.88$; df = 3, n = 40, p = 0.0012; Figure 2.10). This result could be broken down into both the predator presence/absence at each location, and the differences between predator locations. Fish made fewer between patch movements when the predator was located on the edge of the release patch compared to the empty enclosure at the same location ($\chi^2 = 11.56$; df = 1, n = 20, p = 0.0007). Prior to predator exposure at the edge of the release patch, focal fish moved an average of 2.4 ± 0.8 times between patches. In contrast, after the predator was placed in the enclosure, focal fish moved an average of 0.6 ± 0.2 times between patches. There was no significant difference in total number of between-patch movements in contrasting the presence of a predator at the edge of the destination patch and the presence of an empty enclosure at the same location ($\chi^2 = 0.53$; df = 1, n = 20, p = 0.4654). Fish moved between patches significantly less often when the predator was located at the edge of the release patch compared to the presence of the predator at the edge of the destination patch ($\chi^2 = 13.48$; df = 1, n = 20, p = 0.0002). Focal fish exposed to a predator at the edge of the release patch moved 0.6 ± 0.2 times between patches, whereas those exposed to a predator at the edge of the destination patch moved an average of 2.6 ± 0.8 times between patches. Fish associating with larger numbers of conspecifics moved more often between patches than did those in smaller groups ($\chi^2 = 9.60$, df = 1, n = 40, p = 0.0020; Figure 2.11),

although there was no significant interaction between the predator variable and group size.

2.4 Discussion

2.4.1 Release density

I tested two specific hypotheses in the release density trials; that focal fish released with more conspecifics would depart the release patch sooner than those released with fewer conspecifics and that focal fish released with more conspecifics would move more frequently between patches. The results of this experiment demonstrated that these decisions are not made based on one factor, such as initial fish density within a patch, but instead may be affected by multiple interacting factors. Additionally, I found that fish length is a factor in many movement behaviours, and that factors such as group size affect movement decisions by juvenile fish.

Although only a mean patch departure time could be ascertained for the fish released as a single individual, fish released with four conspecifics had longer release patch departure times when associating with larger average group sizes. A similar pattern was reported for spice finches, which remained in patches as a means of maintaining group cohesion (Livoreil and Giraldeau 1997). Juvenile cod that associate with an average of two or three conspecifics may stay longer within the release patch until individuals move from a patch together. The decision to remain in a given patch for longer periods of time may signal a preference to maintain group cohesiveness. At the highest release density (fish released with nine conspecifics)

there was no relationship between average group size and release patch departure time. Overall, my data demonstrate that the amount of time before juvenile Atlantic cod depart a habitat patch is affected by an interaction between initial fish density within a patch and group size. These results likely indicate density-dependent effects (e.g. Laurel et al. 2004), and suggest that group size may be unimportant compared to the overall initial fish density within the patch for determining patch departure times. Previous studies have shown the importance of foraging success in patch departure decisions (DeVries et al. 1989, Stenberg and Persson 2005), however no studies address the questions of patch departure in an aquatic species whose association with complex habitat is largely predator driven. Several studies have shown that juvenile cod experience decreased risk of predation in areas of complex habitat (Linehan et al. 2001, Laurel et al. 2003b). Furthermore, work by Fraser et al. (1996) and Gotceitas et al. (1997) suggest that juvenile cod may be capable of assessing predation risk and utilizing complex habitat to minimize this risk. Spatial analyses suggest that juvenile cod forage outside of eelgrass habitat (Wells 2002, Thistle 2006), indicating that decisions regarding departure from such habitat are not related to food availability within the patch. My study builds upon previous patch departure work by identifying group size and fish density as factors that affect patch departure decisions. Additionally, I have applied the study of aquatic patch departure decisions to a system where foraging success is not the primary motivation for patch associations.

Smaller fish moved between patches less often than larger fish. This pattern may simply reflect physiological limitations; large fish are capable of moving faster than smaller fish. In order to correct for size effects, fish swim speed is often reported

relative to body size, however, I recorded the duration of between-patch movements rather than the specific swim speed of the animal. Recording the duration of the between-patch movements allowed me to document the amount of time spent in the open, including any stops or deviations from a straight path the fish may have adopted while moving between patches. Unfortunately, with no correction for body size, it was not possible to determine the nature of the differences in duration observed for between-patch movements. Speed of movement may be affected by anti-predator behaviour or foraging attempts above and beyond limitations imposed by the physical capabilities of the animal itself (Zollner and Lima 2005). It may be that smaller fish spend longer periods of time moving between patches as a result of increased frequency of anti-predator behaviour, such as "freezing", or remaining motionless. Previous studies have shown that freezing can be an effective anti-predation strategy for fishes (Gotceitas and Colgan 1987, Savino and Stein 1989).

How frequently animals migrate between habitat patches may be a function of factors such as resource patchiness, predator movements, and environmental changes such as temperature shifts. My study shows group size and fish size may also mediate between-patch movement decisions. Teleost fishes experience high mortality rates during the early life history stages (e.g. Peterson and Wroblewski 1984). For Atlantic cod, this mortality can be attributed largely to predation by larger fishes, including conspecifics (Scott and Scott 1988, Linehan et al. 2001). Large juveniles are not generally subject to the same predation pressure as their smaller counterparts (see review by Sogard 1997), suggesting that exposure during between-patch migrations may be lessened for larger animals. Size can positively affect the likelihood of

between-patch movements in birds (Grubb and Doherty 1999), and grouping behaviour has been shown to dilute predation risk for some animals (Treherne 1981, Krebs and Davies 1991, Cresswell 1994). It is therefore reasonable to surmise that these two factors can affect the perceived risk of a given situation and affect potentially risky between-patch movements for juvenile fishes. My study indicates that juvenile Atlantic cod may be able to assess the potential risk of predators based on their own size and the number of conspecifics with which they are associated.

2.4.2 Between-patch distance

I had predicted that fish exposed to increased between-patch distance would wait longer periods of time before departing the release patch, would move between patches at a faster speed, and would complete fewer between-patch movements. My results suggested that between-patch distance plays a role in patch-departure decisions; that increased between-patch distance may increase the movement speed of juvenile Atlantic cod moving between patches and that increased between-patch distance corresponds to a decrease in the frequency of between-patch movements. Overall, my results once again suggested that movement decisions by juvenile cod are affected by a variety of factors.

My study shows that the amount of time juvenile Atlantic cod occupy a release patch before moving to another similar patch is affected significantly by the interaction between fish length, between-patch distance, and group size. This interaction suggests that patch departure decisions may be based on information other than, or in addition to, foraging success or immediate predation threat as shown by previous work (DeVries et al. 1989, Stenberg and Persson 2005). Predation risk for

juvenile cod is higher outside of eelgrass habitat (Linehan et al. 2001), and travelling greater distances outside of protective habitat therefore poses increased risk for migrants. As previously stated, larger fish are less vulnerable to predation than their smaller counterparts (Sogard 1997), so it is reasonable to expect variation in the perceived risk of moving over different distances for fish of different sizes. Grouping behaviour also has the potential to dilute an individual's risk during a predator attack, so it is once again reasonable to infer that group size can affect the perceived risk of migration over an open area and the decision to undertake such a movement. It is therefore not unusual that these three factors play a role in the amount of time a fish spends in a given habitat patch.

My results show that several factors may affect the speed at which fish move between patches of habitat. With increased distance between patches, my results showed a trend towards increased speed of movement when moving between patches. In addition to the weak effect of distance on average speed of movement, my results show a significant interaction of fish length and average group size. The interaction between fish length and average group size was not unexpected given the increased swimming capability of larger fish noted above, and the potential decrease in risk perceived by individuals when associating with larger number of conspecifics. Factors that play a role in the reduction of perceived risk may encourage fish to move more freely and quickly between patches.

As expected, juvenile Atlantic cod reduce their frequency of between-patch movement when presented with increased between-patch distance, suggesting that fish are capable of determining the difference between the two patches. Given that

juvenile Atlantic cod are subject to increased predation risk over open areas (Linehan et al. 2001), I expected that crossing larger distances over bare substrate would increase risk of predation compared to shorter distances. Gotceitas et al. (1995) demonstrated that juvenile Atlantic cod can differentiate between different levels of risk by comparing reactions to an actively foraging or non-actively foraging predator. By reducing the number of between-patch movements at larger between-patch distances, fish modify their behaviour in response to the increased risk of moving between patches. This result supports Gotceitas' finding that juvenile cod are capable of risk assessment, and shows that risk assessment extends to situations other than a direct predator encounter. Moreover, the data presented here demonstrate that fish associated with higher numbers of conspecifics are more likely to move between patches, irrespective of between-patch distance. My results suggest that grouping behaviour may mediate the risk posed by moving over bare substrate. This assertion is consistent with previous work by Laurel et al. (2004), which suggested that juvenile Atlantic cod aggregate over bare substrate as a means of diluting predation risk. My results demonstrate that juvenile cod presented with between-patch distances of differing sizes move fewer times when presented with greater between-patch distances. This type of functional response to gaps in habitat has been identified in several species, particularly birds. Several bird species choose routes through protective cover, even if such routes present a longer travel distance than a direct route through an open area, presumably to avoid exposure to predators (Desrochers and Hannon 1997, Bélisle and Desrochers 2002, Creegan and Osborne 2005). Reed warblers presented with a choice of various gap sizes preferentially select the shortest

possible route to cover, thereby minimizing time in areas with high predation risk (Bosschieter and Goedhart 2005). My work suggests that marine systems are potentially sensitive to habitat fragmentation at even small (metres) scales, and that similarities can be found between the functional responses of marine and terrestrial organisms to gaps in protective cover.

2.4.3 Predator effects

Foraging bluegill sunfish exposed to patches that vary in food and predation risk chose to forage in patches that minimize the ratio of predation rate to foraging rate (Gotceitas 1990). Juvenile black surfperch presented with patches of variable physical structure and predation risk choose patches primarily based on foraging success, where physical structure becomes a factor in patch choice with increased predation risk (Schmitt and Holbrook 1985). The data I have presented here show that the decision to depart a particular patch of habitat is affected by the interaction of predation, fish length, and average group size. This finding reinforces the predator effects on patch departure shown in previous studies (Schmitt and Holbrook 1985, Gotceitas 1990), and suggests that fish assess their own size and the number of companions when deciding to depart habitat patches. It is also clear from these past studies that predation affects movement decisions; however, previous studies have not examined the effects of predation risk on between-patch movement itself.

Previous work on juvenile cod presented with a predator and various substrate combinations show that juvenile cod select complex habitat in the presence of a predator and they are able to distinguish between an actively foraging and non-actively foraging predator (Gotceitas et al. 1995). Gotceitas et al. (1995) also showed

that juvenile Atlantic cod assessed risk based not only on the foraging behaviour of the predator, but also based on their relative location with respect to the predator. The present study builds on these results, indicating that juvenile Atlantic cod respond to predator proximity in different ways. In the absence of a predator, fish that associated with greater numbers of conspecifics (i.e. in larger average group sizes) moved more slowly over the open area between patches than did fish associated with small groups. This result agrees with modelling work that has shown an effect of group size on movement of simulated schools of fish, with larger groups moving more slowly (Romey 1996). Simulations have shown that fish determine their own behaviour largely on the basis of the behaviour of other individuals in the school (Romey 1996). However, the simulations did not include the effects of external stimuli on movement decisions. My study introduced an external stimulus in the form of a predator, which appears to reverse the relationship between group size and movement seen in the absence of the predator. Fish in larger groups moved more quickly when a predator was present in the experimental arena, indicating that movement is regulated by average group size and depends on the predation threat. This behaviour may reflect variability in the effectiveness of different predator avoidance strategies for fish in large or small groups of conspecifics. Smaller groups may be able to avoid detection by a predator by freezing, whereas the same strategy may not be effective for a larger, more conspicuous group. Given the presence of predators in the wild, this result may indicate large schools of juvenile cod are more mobile over larger distances (within and/or between bays), thus contributing to connectivity at the juvenile life stage.

My results support the conclusion that juvenile Atlantic cod will actively avoid a perceived predation threat (Gotceitas et al. 1995) by moving to the other end of the tank, but they also indicate that the presence of a predator may impede movement by juvenile Atlantic cod in highly fragmented habitat, as several juvenile cod tested remained in the release patch when exposed to a predator. The location of a potential predator is important for young fish as they move between patches of protective cover, as demonstrated by the significant decrease in between-patch movements completed by fish exposed to a predator located at the end of the release patch. The presence of the predator at the edge of the destination patch did not have a dampening effect on the total number of between-patch movements, in contrast to the behaviour I observed when the predator was located at the edge of the release patch. This result agrees with Gotceitas et al. (1995), and also suggests that predator proximity and assessment of predation threat can affect fish movement in fragmented habitat.

2.4.4. Implications and conclusions

In summary, my study demonstrates the importance of factors other than foraging in the movement decisions of juvenile fish. While foraging is likely a main reason for fish movement, other factors must be considered as possible mediators of movement behaviour, such as group size, fish length, and predation risk. Studies of terrestrial species have shown that there is reluctance on the part of many animals to cross open areas between patches of complex habitat, and my results demonstrate that there are specific mechanisms that may produce a similar response in a marine species. Furthermore, my study applies techniques that have been used in terrestrial

landscape ecology to examine the effects of habitat fragmentation on movement in a marine species. In addition to the effects of habitat fragmentation on abundance and distribution, this study identifies specific mechanisms that affect distribution at the juvenile life history stage. It should be noted that the focal fish in my laboratory experiments associated with highly fluctuating numbers of conspecifics. While I chose to analyze mean group sizes, it is possible that fluidity in group size may play an additional role in behavioural decisions; a possibility that merits further study. Future experiments would benefit from videotaping the trials to allow for more detailed behavioural observations, but this approach would require overcoming the logistical constraints of accurately videotaping large experimental arenas. Overall, this work suggests that there are likely to be significant ramifications of habitat destruction for juvenile Atlantic cod and other species that move among coastal habitats. These effects are of particular concern in light of declines in complex habitats such as seagrass as a result of natural impacts or anthropogenic effects.

2.5 References

Baker, L. 2007. Effects of corridors on the movement behaviour of the jumping spider *Phidippus princeps* (Araneae Salticidae). Canadian Journal of Zoology 85: 802-808.

Beier, P. 1993. Determining minimum habitat areas and habitat corridors for cougars. Conservation Biology 7: 94-108.

Bélisle, M., Desrochers, A. 2002. Gap-crossing decisions by forest birds: an empirical basis for parameterizing spatially-explicit, individual-based models. Landscape Ecology 17: 219-231.

Bosschieter, L., Goedhart, P.W. 2005. Gap crossing decisions by reed warblers (*Acrocephalus scirpaceus*) in agricultural landscapes. Landscape Ecology 20: 455-468.

Creegan, H.P., Osborne, P.E. 2005. Gap-crossing decisions of woodland songbirds in Scotland: an experimental approach. Journal of Applied Ecology 42: 678-687.

Cresswell, W. 1994. Flocking is an effective anti-predation strategy in redshanks, *Tringa tetanus*. Animal Behavior 47: 433-442.

Crowder, L.B., Cooper, W.E. 1982. Habitat structural complexity and the interaction between bluegills and their prey. Ecology 63: 1802-1813.

Desrochers, A., Hannon, S. J. 1997. Gap crossing decisions by forest songbirds during the post-fledgling period. Conservation Biology 11: 1204-1210.

DeVries, D.R., Stein, R.A., Chesson, P.L. 1989. Sunfish foraging among patches: The patch-departure decision. Animal Behaviour 37: 455-464.

Foster, W.A., Treherne, J.E. 1981. Evidence for the dilution effect in the selfish herd from fish predation in a marine insect. Nature 295: 466-467.

Fraser, S., Gotceitas, V., Brown, J.A. 1996. Interactions between age-classes of Atlantic cod and their distribution among bottom substrates. Canadian Journal of Fisheries and Aquatic Sciences 53: 305-314.

Frid, A. 1997. Vigilance by female Dall's sheep: interactions between predation risk factors. Animal Behavior 53: 799-808.

Gotceitas, V. 1990. Foraging and predator avoidance: a test of a patch choice model with juvenile bluegill sunfish. Oecologia 83: 346-351.

Gotceitas, V., Colgan, P. 1987. Predator foraging success and habitat complexity: quantitative test of the threshold hypothesis. Oecologia, 80: 158-166.

Gotceitas, V., Fraser, S., Brown, J.A. 1997. Use of eelgrass beds (*Zostera marina*) by juvenile Atlantic cod (*Gadus morhua*). Canadian Journal of Fisheries and Aquatic Sciences 54: 1306-1319.

Gotceitas, V., Fraser, S., Brown, J.A. 1995. Habitat use by juvenile Atlantic cod (*Gadus morhua*) in the presence of an actively foraging and non-foraging predator. Marine Biology 123: 421-430.

Grant, S.M., Brown, J.A. 1998. Nearshore settlement and localized populations of age-0 Atlantic cod (*Gadus morhua*) in shallow coastal waters of Newfoundland. Canadian Journal of Fisheries and Aquatic Sciences 55: 1317-1327.

Grubb Jr., T.C., Doherty Jr., P.F. 1999. On home-range gap-crossing. The Auk 116: 618-628.

Kopp, K., Wachlevski, M., Eterovick, P.C. 2006. Environmental complexity reduces tadpole predation by water bugs. Canadian Journal of Zoology 84: 136-140.

Krebs, J.R., Davies, N.B. 1991. Behavioral Ecology 3rd Edn. Blackwell Scientific. Boston.

Laurel, B.J., Gregory, R.S., Brown, J.A. 2003 (a). Settlement and distribution of Age-0 juvenile cod, *Gadus morhua* and *G. ogac*, following a large-scale habitat manipulation. Marine Ecology Progress Series 262: 241-252.

Laurel, B.J., Gregory, R. S., Brown, J.A. 2003 (b). Predator distribution and habitat patch area determine predation rates on age-0 Atlantic cod, *Gadus* spp. Marine Ecology Progress Series 251: 245-254.

Laurel, B.J., Gregory, R.S., Brown, J.A., Hancock, J.K., Schneider, D.C. 2004. Behavioural consequences of density-dependent habitat use in juvenile cod *Gadus morhua* and *G. ogac*: the role of movement and aggregation. Marine Ecology Progress Series 272: 257-270.

Lima, S.L., Dill, L.M. 1990. Behavioural decisions made under the risk of predation: a review and prospectus. Canadian Journal of Zoology 68: 619-640.

Linehan, J.E., Gregory, R.S., Schneider, D.C. 2001. Predation risk of age-0 cod (*Gadus*) relative to depth and substrate in coastal waters. Journal of Experimental Marine Biology and Ecology 263: 25-44.

Lingle, S. 2001. Anti-predator strategies and grouping patterns in white-tailed deer and mule deer. Ethology 107: 295-314.

Livoreil, B., Giraldeau, L.A. 1997. Patch departure decisions by spice finches foraging singly or in groups. Animal Behaviour 54: 967-977.

Lough, R.G., Bolz, G.R. 1989.The movement of cod and haddock larvae onto the shoals of Georges Bank. Journal of Fish Biology 35(Supplement A): 71-79.

Martella, M.B., Renison, D., Navarro, J.L. 1995. Vigilance in the greater rhea: effects of vegetation height and group size. Journal of Field Ornithology 66: 215-220.

Methven, D.A., Bajdik, C. 1994. Temporal variation in size and abundance of juvenile Atlantic cod (*Gadus morhua*) at an inshore site off eastern Newfoundland. Canadian Journal of Fisheries and Aquatic Sciences 51:78-90.

Orth, R.J., Heck, K.L., van Montfrans J. 1984. Faunal communities in seagrass beds: A review of the influence of plant structure and prey characteristics on predator: prey relationships. Estuaries 7: 339-350.

Peterson, I., Wroblewski, J.S. 1984. Mortality rate of fishes in the pelagic ecosystem. Canadian Journal of Fisheries and Aquatic Sciences 41: 1117-1120.

Pierce, B.M., Bowyer, R.T., Bleich, V.C. 2004. Habitat selection by mule deer: foraging benefits or risk of predation? Journal of Wildlife Management 68: 533-541.

Pitcher, T. J. 1986. Functions of shoaling behaviour in teleosts. In: Behaviour of Teleost Fishes (Ed. by T. J. Pitcher), pp. 294-337. Baltimore: Johns Hopkins University Press.

Romey, W.L. 1996. Individual differences make a difference in the trajectories of simulated schools of fish. Ecological Modelling 92: 65-77.

Savino, J.F., Stein, R.A.. 1989. Behavioural interactions between fish predators and their prey: effect of plant density. Animal Behaviour. 37: 311-321.

Savino, J.F., Stein, R.A. 1982. Predator-prey interaction between large-mouth bass and bluegills as influenced by simulated, submerged vegetation. Transactions of the American Fisheries Society 111: 255-266.

Schmitt, R.J., Holbrook, S.J. 1985. Patch selection by juvenile black surfperch (*Embiotocidae*) under variable risk: interactive influence of food quality and structural complexity. Journal of Experimental Marine Biology and Ecology 85: 269-285.

Scott, W.B., Scott, M.G. 1988. Atlantic Fishes of Canada. Canadian Bulletin of Fisheies and Aquatic Sciences 219: 713 pp.

Sheppard, G.L. 2005. Natural mortality and movement of juvenile cod (*Gadus* spp.) inhabiting eelgrass (*Zostera marina*) in coastal Newfoundland waters. MSc Thesis, Department of Biology, Memorial University of Newfoundland.

Sogard, S.M. 1997. Size-selective mortality in the juvenile stage of teleost fishes: a review. Bulletin of Marine Science 60: 1129-1157.

Sogard, S.M. 1989. Colonization of artificial seagrass by fishes and decapod crustaceans: importance of proximity to natural eelgrass. Journal of Experimental Marine Biology and Ecology 133: 15-37.

Sogard, S.M., Olla, B.L. 1993. The influence of predator presence on utilization of artificial seagrass habitats by juvenile walleye pollock, *Theragra chalcogramma*. Environmental Biology of Fishes 37: 57-65

Stenberg, M., Persson, A. 2005. The influence of spatial food distribution and group size on foraging behaviour of a benthic fish. Behavioural Processes 70: 41-50.

Thistle, M. E. 2006. Distribution and risk-sensitive foraging of juvenile gadids in relation to fractal complexity of eelgrass (*Zostera marina*) habitat. MSc Thesis. Memorial University of Newfoundland, St. John's, NL.

Tull, J.C., Krausman, P.R. 2001. Use of a wildlife corridor by desert mule deer. The Southwestern Naturalist 46: 81-86.

Tupper, M., Boutilier, R.G. 1995. Effects of habitat on settlement, growth, and postsettlement survival of Atlantic cod (*Gadus morhua*). Canadian Journal of Fisheries and Aquatic Sciences 52: 1834-1841.

Wells, N.J. 2002. Scaling eelgrass complexity in Newman Sound, Newfoundland, and applications to fish ecology. MSc Thesis. Memorial University of Newfoundland, St. John's, NL.

Wrona, F.J., Jamieson Dixon, R.W. 1991. Group size and predation risk: A field analysis of encounter and dilution effects. The American Naturalist 137: 186-201.

Zollner, P.A., Lima, S.L. 1999. Illumination and the perception of remote habitat patches by white-footed mice. Animal Behaviour 58: 489-500.

Zollner, P.A., Lima, S.L. 2005. Behavioural trade-offs when dispersing across a patchy landscape. Oikos 108: 219-230.

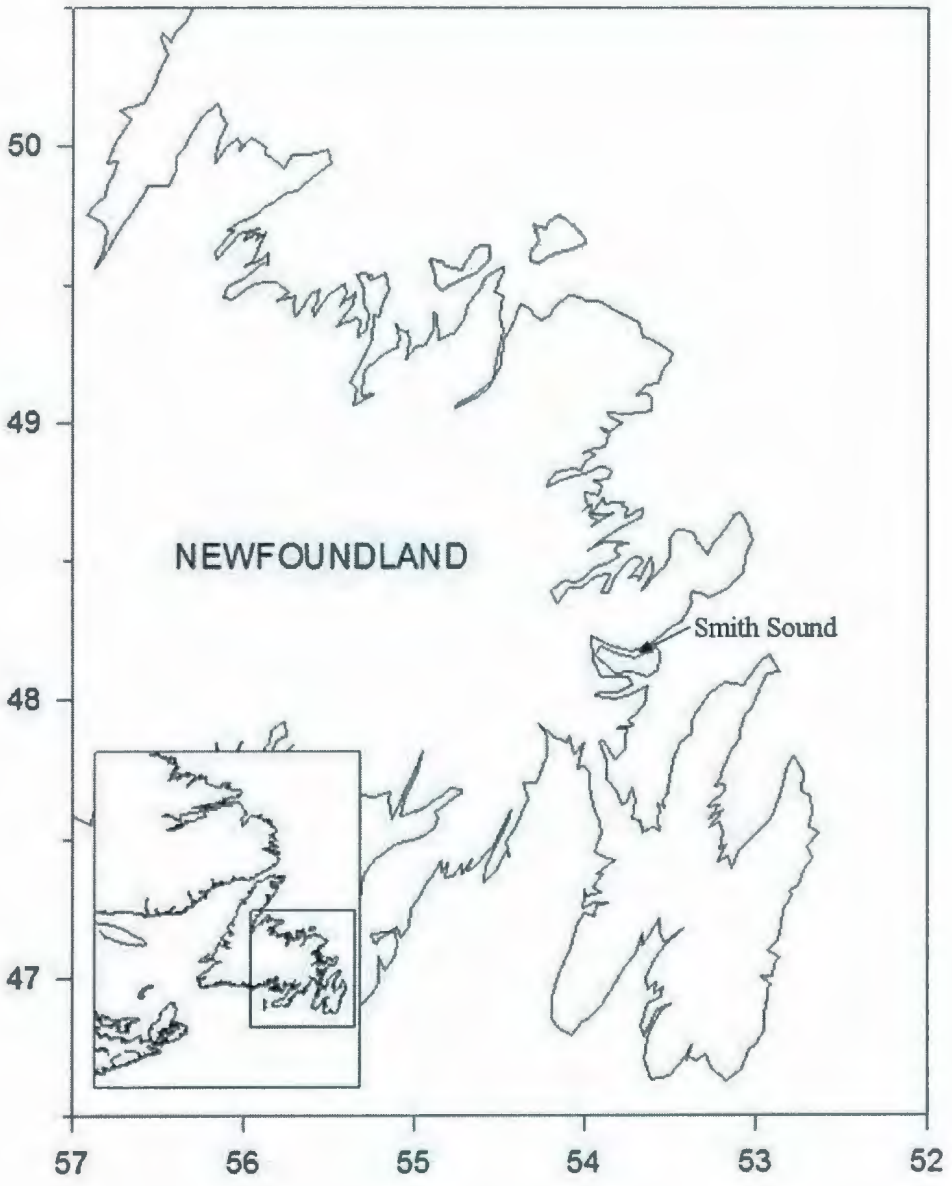

Figure 2.1: Collection site for juvenile Atlantic cod

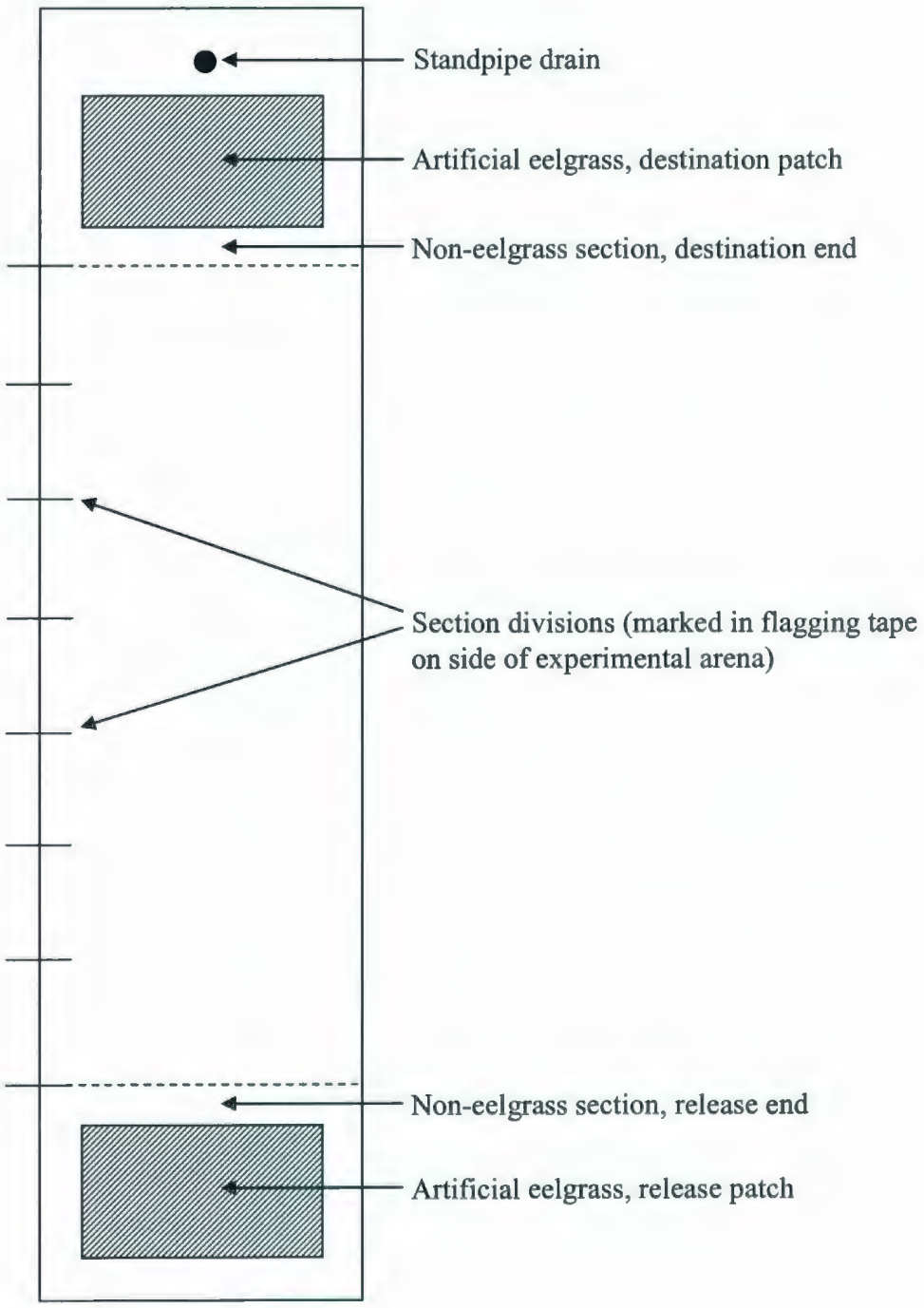

Figure 2.2: Top view of experimental arena (12 m x 3 m x 1.5 m) set-up for release density experiment, showing patch locations and section divisions used to identify fish location within the tank

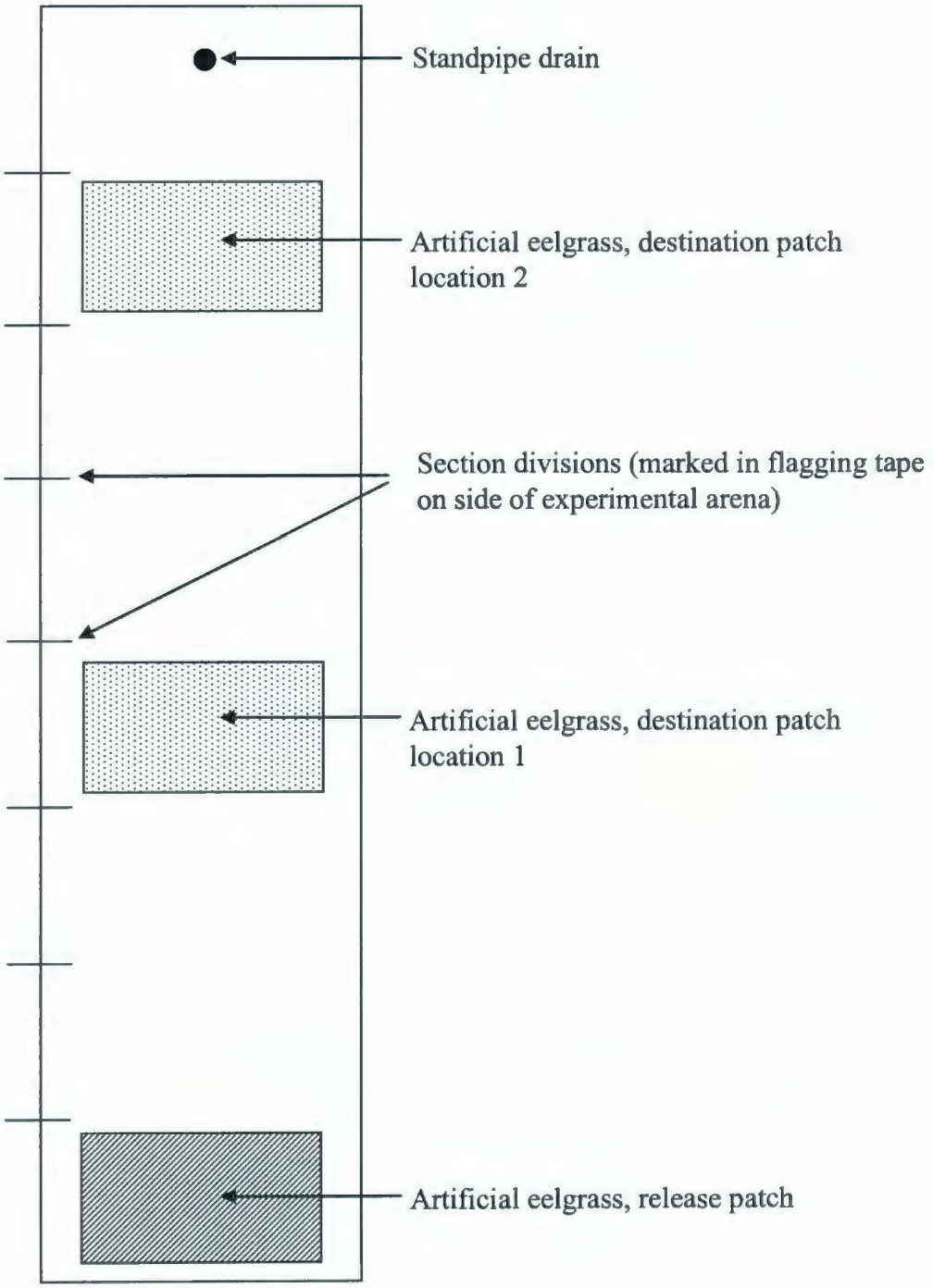

Figure 2.3: Top view of experimental arena (12 m x 3 m x 1.5 m) set-up for between-patch distance experiment, showing patch locations for the two distances tested and section divisions used to identify fish location within the tank

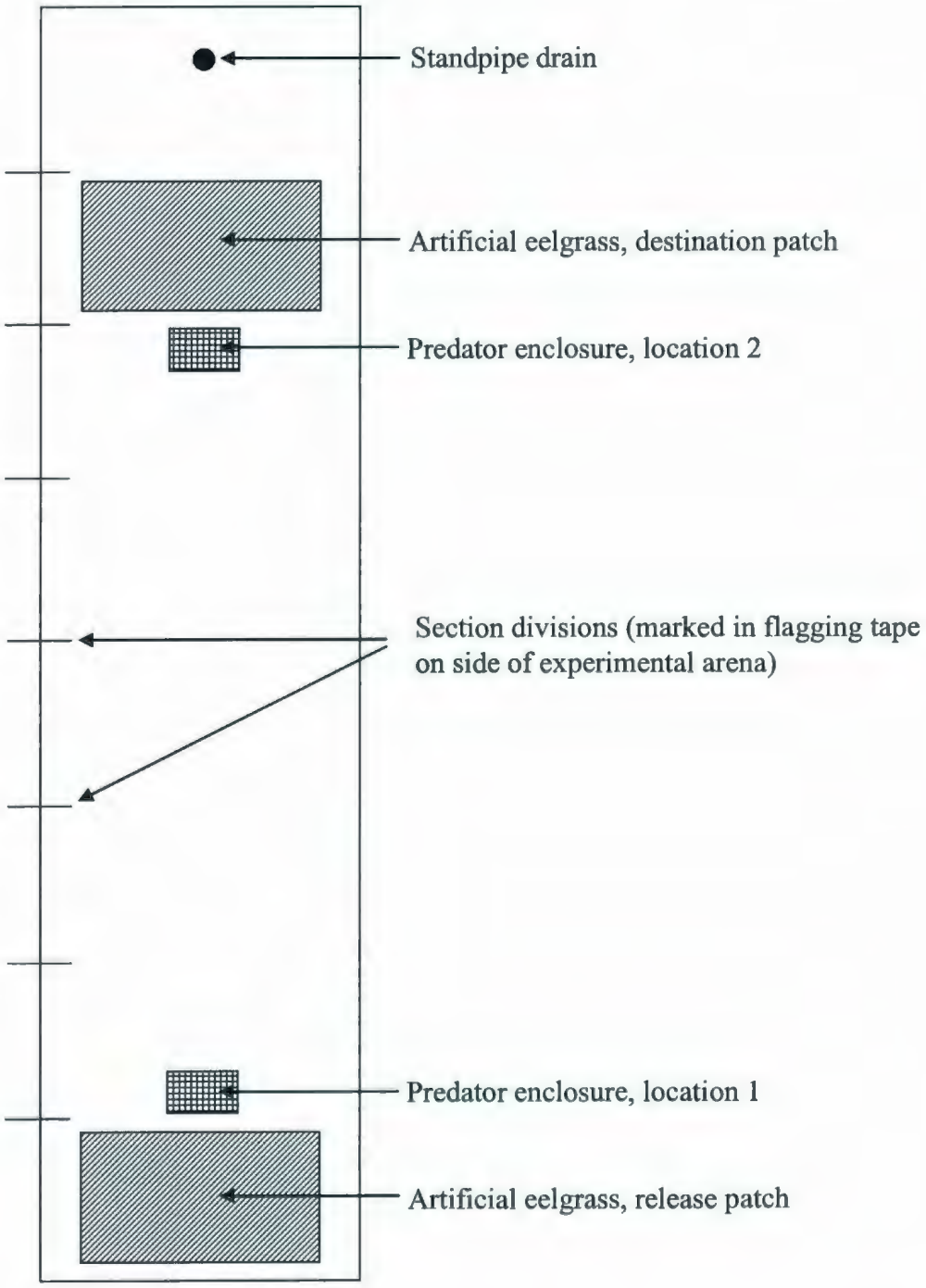

Figure 2.4: Top view of experimental arena (12 m x 3 m x 1.5 m) set-up for predator experiment, showing patch locations, the two predator locations, and section divisions used to identify fish location within the tank

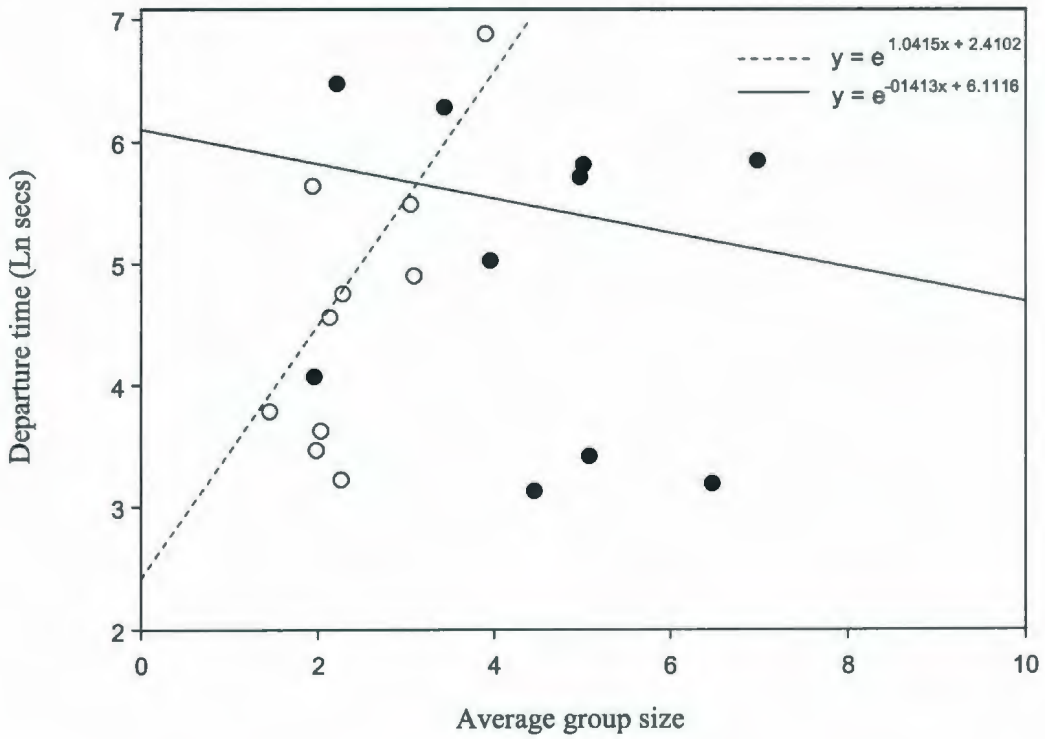

Figure 2.5: Release patch departure time plotted against the average group size for juvenile Atlantic cod released with either four conspecifics (open circles and dashed line) or nine conspecifics (filled circles and solid line) and exposed to a between-patch distance of 8 m

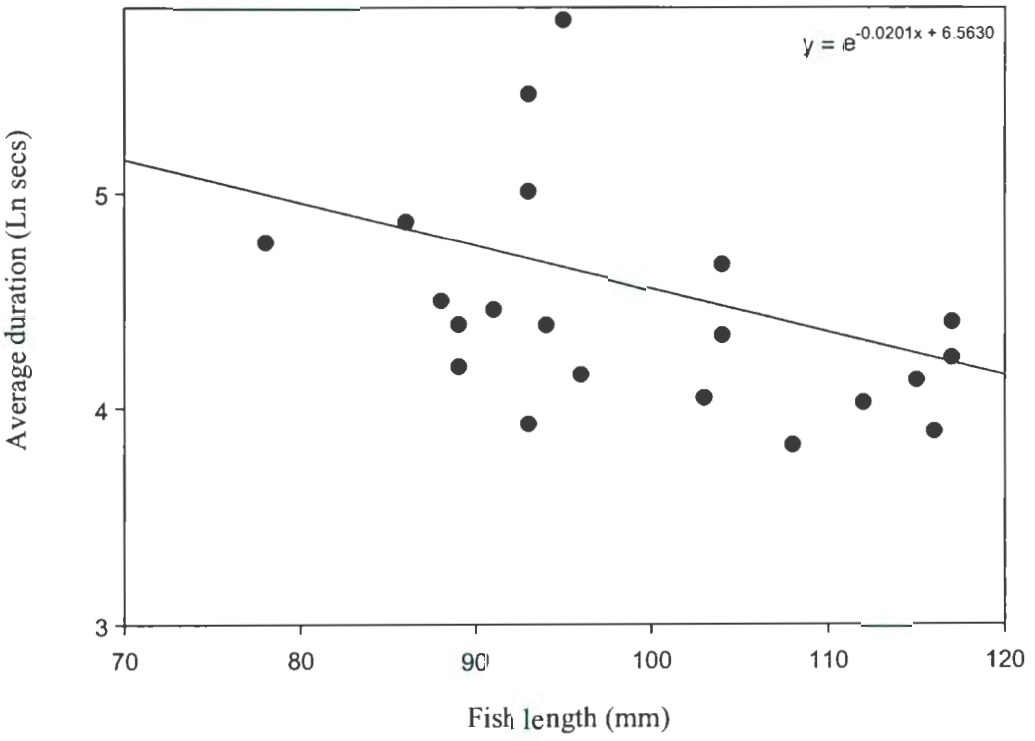

Figure 2.6: Average duration of completed between-patch movements by juvenile Atlantic cod, regardless of release density and exposed to a between-patch distance of 8 m

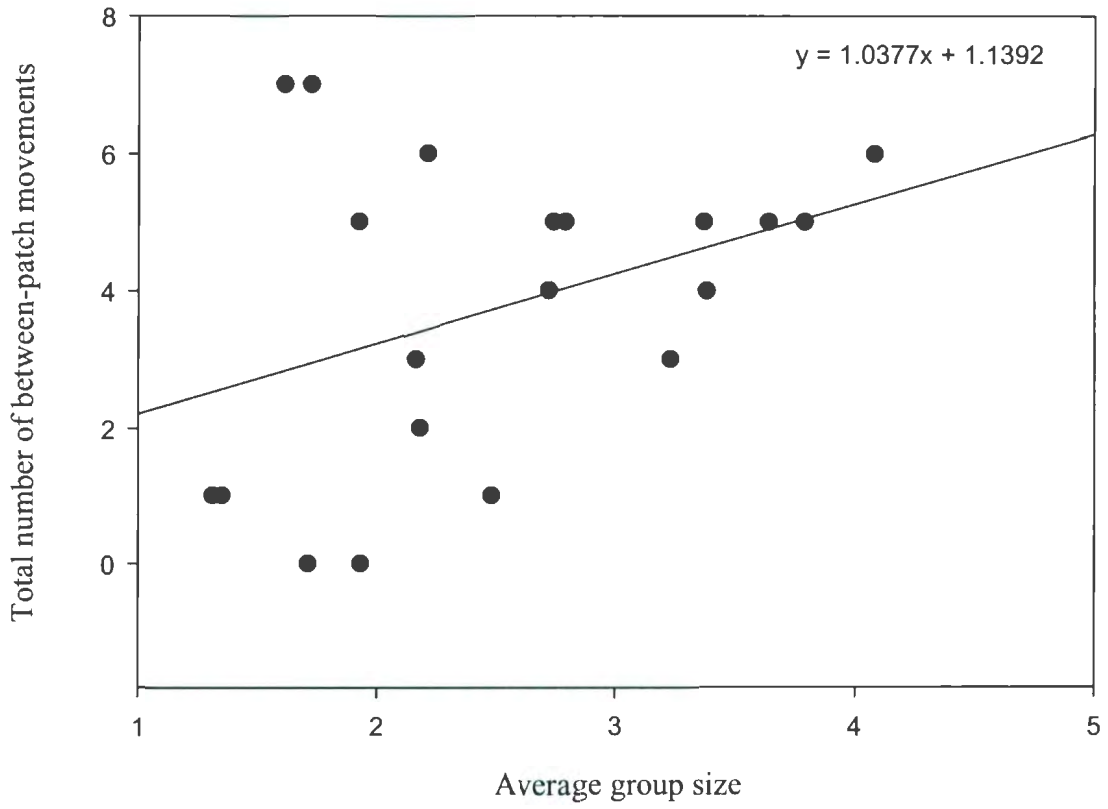

Figure 2.7: Total number of between-patch movements completed by juvenile Atlantic cod regressed against average group size, regardless of between-patch distance

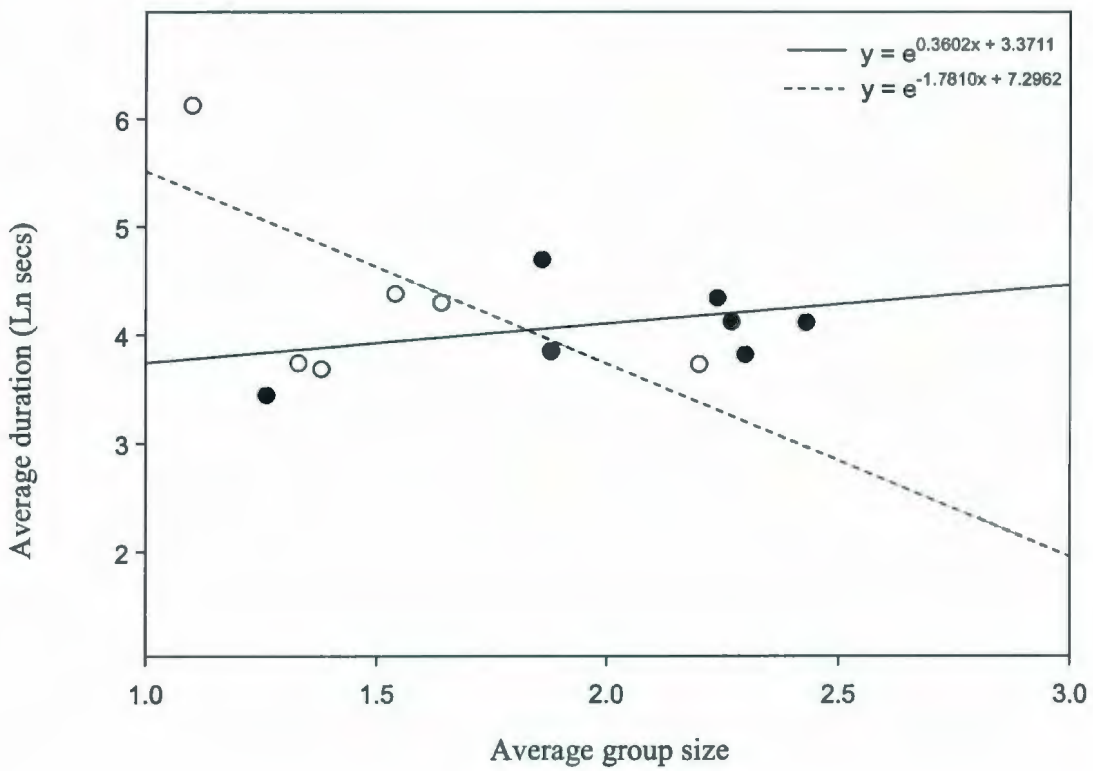

Figure 2.8: Average duration of completed between-patch movements regressed against average group size for juvenile Atlantic cod exposed to a control (filled circles and solid lines) and a predator (open circles and dotted line) on the edge of the release patch

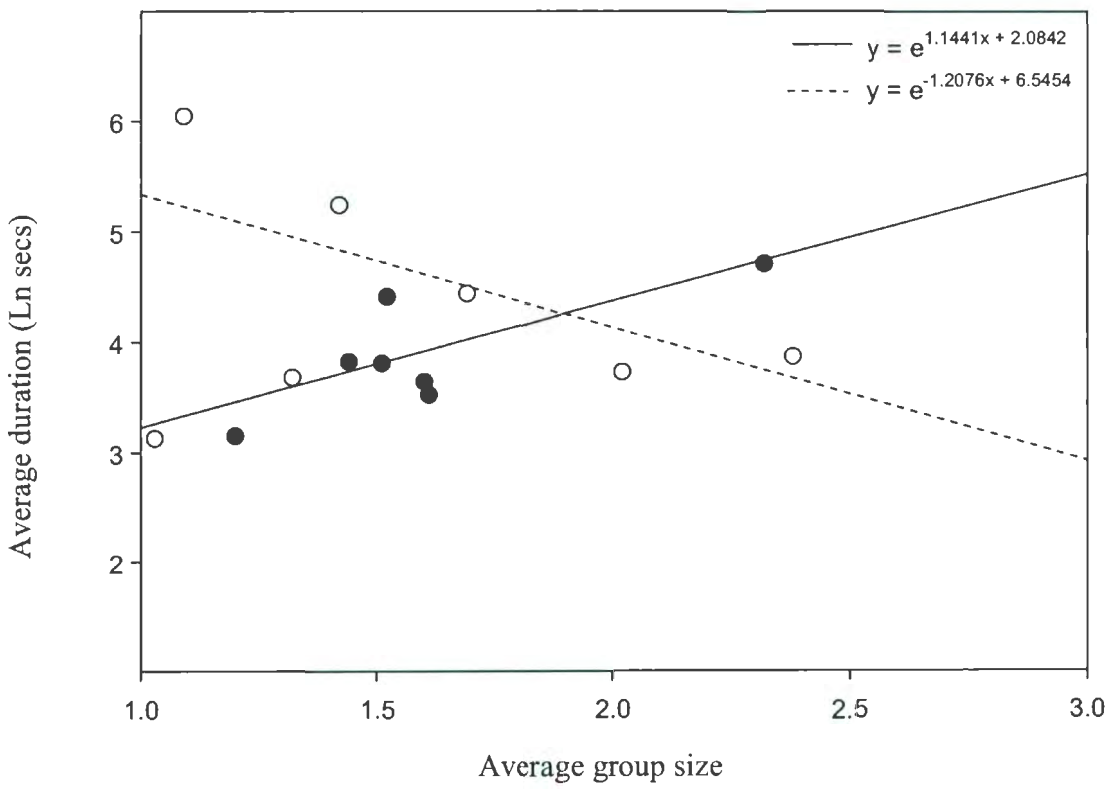

Figure 2.9: Average duration of completed between-patch movements regressed against average group size for juvenile Atlantic cod exposed to a control (filled circles and solid lines) and a predator (open circles and dotted line) on the edge of the destination patch

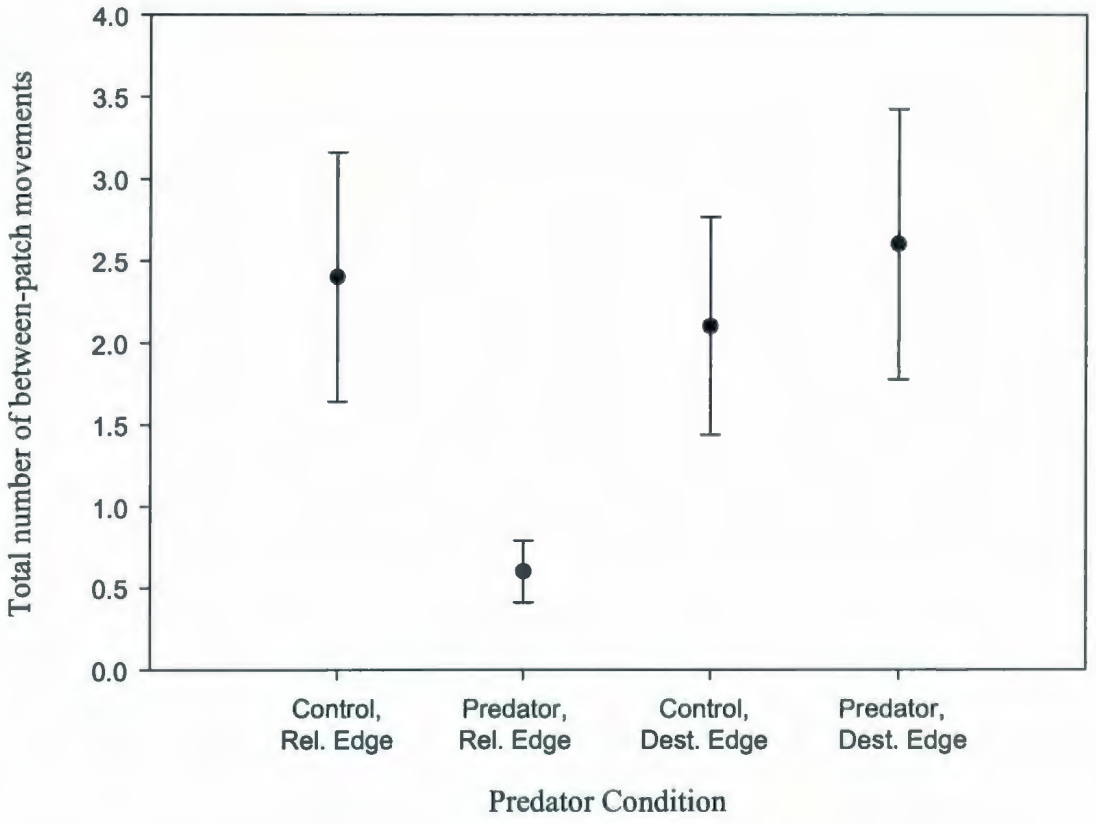

Figure 2.10: Total number of completed between-patch movements (± SE) for juvenile Atlantic cod exposed to a between-patch distance of 7.5 m and a predator or empty predator enclosure at one of two locations

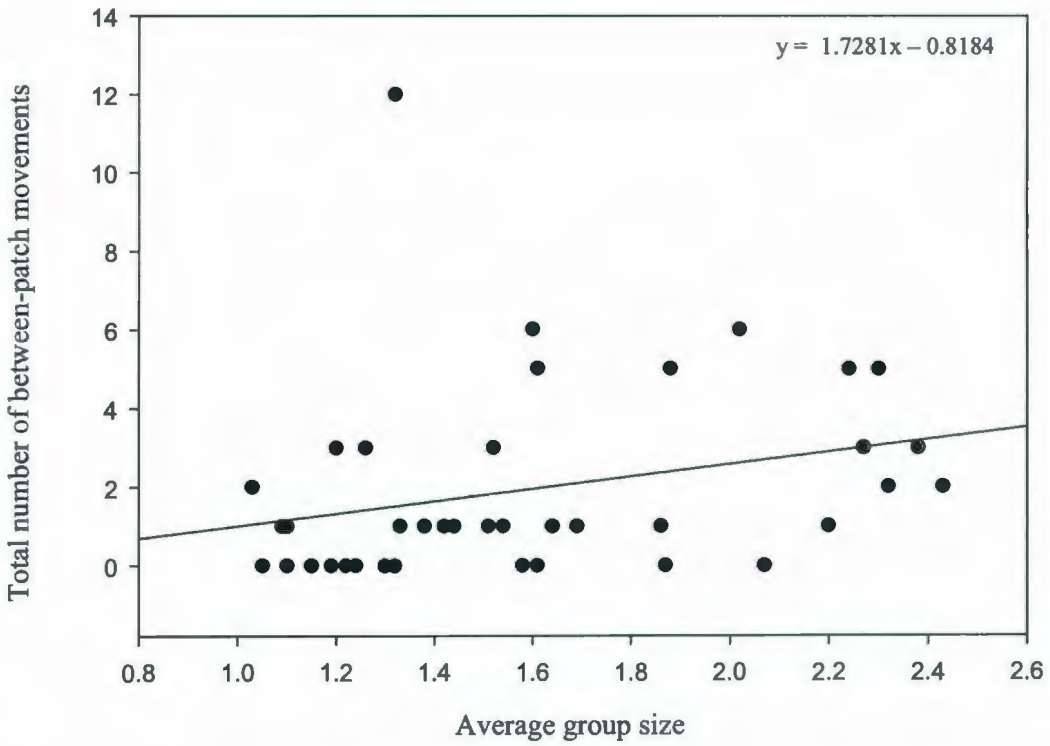

Figure 2.11: Total number of completed between-patch movements regressed against average group size for juvenile Atlantic cod exposed to a between-patch distance of 7.5 m and regardless of predator presence/absence

Appendix 1

Printout of SAS proc GENMOD results for a full model including all explanatory variables and interactions potentially affecting duration of between-patch movements

Model: durcross = condition length avggroup condition*length condition*avggroup length*avggroup condition*length*avggroup

The GENMOD Procedure

Model Information

Distribution	Gamma
Link Function	Log
Dependent Variable	durcross

Criteria For Assessing Goodness Of Fit

Criterion	DF	Value	Value/DF
Deviance	9	4.0296	0.4477
Scaled Deviance	9	25.6529	2.8503
Pearson Chi-Square	9	3.2181	0.3576
Scaled Pearson X2	9	20.4867	2.2763
Log Likelihood		-117.1425	

Algorithm converged.

LR Statistics For Type 3 Analysis

Source	DF	Chi-Square	Pr > ChiSq
condition	3	6.15	0.1043
length	1	0.95	0.3309
avggroup	1	1.00	0.3167
length*condition	3	3.80	0.2839
avggroup*condition	3	3.32	0.3442
length*avggroup	1	1.01	0.3157
length*avggro*condit	3	2.33	0.5072

Chapter 3: Description of inter-patch movement by juvenile cod (*Gadus* spp.) in a coastal Newfoundland fjord: a mark-recapture study

3.1 Introduction

Different species of fish may vary greatly with respect to the spatial range of their movement. Some species display small scales of movement (kilometres or less) through much of their life history. For example, shorthorn sculpin *Myoxocephalus scorpius* have a sessile egg phase and an adult stage that appears to be characterized by high site fidelity (Ennis 1970, Scott and Scott 1988, Luksenburg and Pedersen 2002). Other species such as tuna may exhibit highly mobile life stages from pelagic eggs and larvae that disperse with oceanic currents to adults that forage over distances ranging in the hundreds of kilometres (Stokesbury et al. 2007, Tanaka et al. 2007). Scales of movement at different stages of an animal's ontogeny may also vary. For species such as Atlantic cod *Gadus morhua*, scales of movement may differ among life stages as individuals develop from pelagic egg and larval phases with movement at scales of kilometers, to settlement as juveniles that exhibit movement of hundreds of meters, and finally to the adult phase that exhibits seasonal migrations (Templeman 1979, Scott and Scott 1988, deYoung and Rose 1993).

With the collapse of the commercial cod fishery in the northwest Atlantic Ocean in the early 1990s (Hutchings and Myers 1994), attention has focused on understanding the ecology of inshore cod populations and their potential to contribute to rebuilding inshore and offshore stocks (Hutchings et al. 1993, Morris and Green 2002, Wroblewski and Hiscock 2002). These fish overwinter in coastal embayments then spawn in the spring, both within these embayments and along the coast as they

move out of the overwintering grounds and complete their summer migration along the coast (Wroblewski et al. 1994, Ruzzante et al. 2000, Morris and Green 2002). Juveniles settle into nearshore areas (Grant and Brown 1997), where they remain for the majority of their first two years of life before moving into deeper water as they grow into adults (Dalley and Anderson 1997, Cote et al. 2004). The nature of the life-history of Atlantic cod allows numerous opportunities for the intermixing of individuals from 'separate' populations (i.e. inshore and offshore populations or populations from different bays), and suggests that specific ontogenetic stages might contribute differently to between-bay and within-bay connectivity of cod populations. Such variability in potential connectivity between different populations may have consequences for stock recovery and therefore, management of fisheries. During the juvenile stage, Atlantic cod movement in the nearshore environment has been studied extensively with respect to their range of movement and dispersal from a given location, with varying results. Tupper and Boutilier (1995) and Sheppard (2005) both identified high site fidelity for juveniles, while Laurel et al. (2004) indicated that there were potentially greater scales of movement at the juvenile level in at least some years. However, these studies focused on juvenile cod movement either within continuous protective habitat (Laurel et al. 2004, Sheppard 2005) or without quantifying the potential effects of habitat fragmentation on movement (Tupper and Boutilier 1995, Laurel et al. 2004).

Habitat fragmentation has been shown to be a potential barrier to movement and connectivity in several species, including spiders *Phidippus princeps* (Baker 2007), cougars *Felis concolor* (Beier 1993), mice *Peromyscus leucopus* (Zollner and

Lima 1999), and songbirds (Creegan and Osborne 1995). Juvenile cod living in coastal areas associate with eelgrass *Zostera marina*, a species of seagrass that exhibits a high degree of natural fragmentation in its growth patterns (Robbins and Bell 1994). Juvenile cod associate with eelgrass as a means of reducing predation (Gotceitas et al. 1997, Linehan et al. 2001, Laurel et al. 2003b). Gotceitas et al. (1997) showed that juvenile cod select non-eelgrass habitat prior to exposure to a predator, but select eelgrass during predator exposure. Additionally, predation rates for juvenile cod are higher outside of eelgrass patches than within (Linehan et al. 2001), and predation on juvenile cod depends on patch size in eelgrass habitat, with fish in larger patches experiencing lower rates of predation than those in smaller patches (Laurel et al. 2003b). These studies suggest that eelgrass patch structure influences the benefit that eelgrass provides to Atlantic cod juveniles. They also suggest that there may be motivation for juvenile Atlantic cod to reduce the frequency of movement when moving outside protective eelgrass habitats relative to movement within a protective habitat matrix. Consequently, studies of juvenile cod movement that are conducted only in continuous eelgrass habitat, or without accounting for the potential effects of habitat fragmentation, may overestimate the likelihood of juvenile Atlantic cod movement. Juvenile cod may move outside of protective habitat for various reasons including foraging, temperature changes, predator presence or exploration.

I utilized mark-recapture techniques to describe movement by juvenile Atlantic cod introduced in a field setting to protective habitat patches separated by various distances over either bare substrate or areas of natural protective habitat. The

intent of this experiment was to identify differences in the rate of movement out of areas with different habitat characteristics (i.e. comparing flux rates between two habitats). For this experiment I expected higher movement rates out of barren sites compared to sites with protective habitat patches. I also describe two further experiments on Greenland cod *Gadus ogac* that attempted to determine the effects of between-patch distance and patch size on movement in a fragmented landscape. Greenland cod were used in these experiments due to low recruitment of juvenile Atlantic cod in the study area during 2006 (Gregory et al. 2006, pers. obs.). I expected that increasing between-patch distance would result in less between-patch movement, and fish exposed to patches of varying sizes would be more likely to move to larger patches of eelgrass.

3.2 Methods

3.2.1 Study site

I conducted mark-recapture work in 2006 and 2007 in Newman Sound, a glacial fjord located in Bonavista Bay on the northeast coast of Newfoundland, Canada (Figure 3.1). The fjord is approximately 41 km long, and ranges from 1.5 km to 3.0 km wide. It has an inner and outer basin separated by a sill 18 m deep located approximately 7 km from the head of the fjord. Maximum water depth in the inner basin is 55 m, in contrast to over 300 m in the outer basin. Substrate in the nearshore ranges from mud to bedrock. Macroalgae (*Laminaria digitata*, *Agarum cribrosum*, *Chondrus crispus*, *Fucus vesiculosus,* and *Ascophyllum nodosum*) and eelgrass comprise the predominant vegetation. Where present, eelgrass grows in sandy and

muddy substrate of the subtidal zone, to a water depth of approximately 5 m – 6 m. Water temperatures in the study area range from 20 °C in August to -1 °C in December.

A small cove on the southern side of the outer sound was selected as the main study site. Big Cold East (48° 34' N, 53° 49' W; Figure 3.1) is characterized by cobble and mud substrate with no eelgrass growth (presumably as a result of ice scour in the winter months). I chose this site because it had no eelgrass and much of coastline could be sampled by seine, in contrast with other coves in the sound where seining would have been limited or impossible due to rocky coastline. The cove is 300 m long and ranges from 40 m - 132 m wide with a maximum water depth of 6 m. I identified two additional sites, adjacent to Big Cold East, which were monitored to identify larger-scale (i.e. beyond a single cove) movements of Atlantic cod. These two "bracketing sites" were Little Cold East (48° 34' N, 53° 49' W, located 1 km north of the study site; Figure 3.1) and South Broad Cove (48° 33' N, 53° 51' W located 2.5 km southwest of the study site; Figure 3.1). These sites were characterized by contiguous eelgrass. Finally, I used a long beach on the western side of the inner portion of the sound (48° 35' N, 53° 55' W; Figure 3.1) as an additional study site for the flux rate comparison study in 2007. This beach (Bermuda Beach) was characterized by contiguous eelgrass meadows.

3.2.2 Artificial eelgrass patches

I constructed patches of artificial eelgrass by affixing green polypropylene ribbon (width = 4.7 mm, length = 75 cm) to a wire mesh base at a density of 700 stems per square metre (method based on Laurel et al. 2003a). This density is within

the range of natural eelgrass densities (Orth et al. 1984, Gotceitas et al. 1997), and artificial eelgrass has been shown to adequately mimic natural eelgrass in habitat studies (e.g. Sogard and Olla 1993, Gotceitas et al. 1997, Laurel et al. 2003a). Patches were affixed to the substrate of the study site along the shoreline in varying configurations depending on the specific experiment (see descriptions below).

3.2.3 Beach seining

Juvenile cod were collected by beach seining (modified from Lear et al. 1980, Methven and Schneider 1998). The gear consisted of a 25 m modified Danish bag seine, with 19 mm stretch mesh, a 24.4 m headrope, and a 26.2 m footrope. Each wing had a 75 cm long aluminum spreading bar, which was 25 mm in diameter. The seine was deployed from a 6 m boat approximately 55 m offshore and retrieved by two people standing onshore approximately 16 m apart. A leaded footrope and floats on the headrope allowed the seine to drag along the bottom while sampling 2 m up into the water column, providing an overall sampling area of 880 m^2. SCUBA observations have determined that seining captures 95% of fish in the sampling area (Gotceitas et al. 1997). During the summer and fall of 2006 and the fall of 2007, fish were collected using a beach seine from various sites in inner Newman Sound or in Big Cold East. Atlantic cod or Greenland cod (depending on experiment – see below) were separated and identified to age class using established age-length relationships (Gregory et al. 2000). Age-0 cod were retained for experiments whereas all other fish were released back into the collection site. Cod were then held for up to 24 hours in one of two 72 L holding tanks that were placed on the bottom of Newman Sound at a water depth of approximately 4 m. Panels of plastic mesh were affixed to four 10 cm

by 30 cm openings that were cut in the tanks to allow water exchange. After the holding period, I transferred all fish to large tubs filled with seawater, where they were held prior to tagging and release.

3.2.4 Tagging and release of juvenile cod

I double tagged all fish, first with a dye mark on the ventral surface between the pectoral fins, using a PanJet Injector (™ Northwest Marine Technologies), and then by insertion of Visual Implant alphanumeric (VI Alpha™; Northwest Marine Technologies Inc., Shaw Island WA, USA). VI Alpha tagging involves insertion of a 1.0 x 2.5 mm rectangular tag beneath transparent tissue with a modified syringe injector. Each tag is labelled with a unique three digit code that consists of one letter and two numbers. Tagging protocol consisted of panjet marking all fish so that individuals involved in the study could be quickly identified, and then placing individuals in a large recovery tub filled with seawater. I then removed each individual from the recovery bucket, inserted a VI Alpha tag under the skin on the left side of the dorsal fin, and measured the fish to the nearest mm standard length (SL). All fish were then placed in a wire mesh cage submerged in a 70 L bucket of seawater. Fish were held in the holding buckets, which were covered and regularly refreshed with seawater to maintain dissolved oxygen levels, until release (approximately 2 hours). In 2007 I discontinued panjet marking of fish because it was unnecessary given the high visibility of the VI Alpha tags. Tagging consisted of VI Alpha tag insertion, a recovery period of at least 2 hours in the mesh cages submersed in seawater, and then release into the study area. Fish were released in a wire mesh cage that opened automatically approximately 30 minutes after deployment following

the dissolving of the Lifesavers™ candy that held the escape door shut. This remote release allowed fish to move into the adjacent habitat patch without direct mechanical manipulation of the cage by observers, defined a uniform release location, and minimized any flight response behaviour by experimental animals.

3.2.5 Recapture

Recapture was attempted with a beach seine, noting that the area sampled by the seine was reduced so that only the habitat patches themselves were sampled. The seine was deployed offshore to a distance just sufficient to encompass the target patch, prior to retrieval by two individuals standing side by side on the shoreline. This method ensured that only the habitat patch itself was sampled, with minimal sampling of the surrounding substrate.

3.2.6 Experimental Design – Effects of between-patch distance on Greenland cod movement between eelgrass patches

Artificial eelgrass patches 5 m^2 in area were affixed to the substrate in Big Cold East at a depth of approximately 2 m (Figure 3.2). Five pairs of patches were deployed so that the patches in each pair were separated from each other by a different distance (5 m, 10 m, 20 m, 40 m, or 50 m). Each patch pair was separated from the nearest patch pair by at least the distance between the two patches in a given pair (e.g. the pair of patches separated by 30 m was located at least 30 m from any other pair), except for the 50 m pair; one patch in the 50 m pair was located approximately 30 m from the nearest patch in the next adjacent patch pair. Larger spacing was not possible because of space limitations at the study site. Prior to deployment of patches, seining was conducted at several locations within the study

site to determine which species were common prior to habitat modification. Six sites were seined, yielding a total of 20 fish that included age-1 Atlantic cod, age-1 Greenland cod, cunner *Tautogolabrus adspersus*, sculpin *Myoxocephalus scorpius*, stickleback *Gasterosteus aculeatus,* and winter flounder *Pseudopleuronectes americanus*. Six weeks after patch deployment and prior to any mark-recapture trials, four seine hauls at the study site captured a total of 109 fish, including stickleback, white hake *Urophycis tenuis*, winter flounder, cunner, age-1 Greenland cod, and age-1 Atlantic cod. One week prior to the beginning of the mark-recapture trials, each of the patches were seined to ensure that the seine would not snag on the patches, and to assess the species present at the site prior to addition of tagged fish. I found several species were present, including cunner, stickleback, white hake, rock crab *Cancer irroratus*, age-1 Greenland cod, age-0 Greenland cod and age-0 Atlantic cod. Immediately preceding release of tagged fish into the site, each of the eelgrass patches were seined, in addition to the open area between each pair of patches. I recorded the species and size (standard length, SL) of each fish captured in the seines prior to releasing all fish back into the study area. I tagged all fish that were > 15 cm (SL) by inserting a Floy T-bar tag (™ Hallprint Pty Ltd) into the dorsal musculature of the fish just below the dorsal fin. These tags identified potential predators within the study site and allowed me to determine whether predators remained in the study area for extended periods of time or whether they were transient.

For the mark-recapture trials, I released 10 age-0 Greenland cod into a randomly-selected patch from each pair of patches ("release patches") using the release method described above. This resulted in a total release of 50 fish over five

patches. Twenty-four hours following release, all eelgrass patches and the bare area between the patches in each pair were seined. I examined all juvenile Greenland cod for surgical wounds from tag insertion and VI Alpha tags, and identified and measured all fish caught in the seine. This procedure was repeated on three separate days in August 2006.

After recapturing few tagged fish, I completed one further replication of the above experiment in September of 2006, although I shortened the time before attempting recapture to 3 hours. This reduction in the time between release and recapture seining allowed me to test whether time-at-large affected likelihood of recapture.

3.2.7 Experimental Design – Effects of patch size and residency on odds of Greenland cod movement between eelgrass patches

Four eelgrass patches, two 5 m^2 in area and two 20 m^2 in area, were deployed at my study site at approximately 2 m depth (Figure 3.3). The patches were deployed in relation to a single, central "release point". A 5 m^2 eelgrass patch was deployed 30 m north of the release point, and a 20 m^2 patch was deployed 30 m north of that. Similarly, two patches were deployed south of the release point, with the 20 m^2 patch 30 m from the release point and the 5 m^2 patch 30 m beyond that. Control locations for seining were located between the pair of patches north and south of the release point, outside of the outermost patches north and south of the release point, and at the release point itself (see Figure 3.3).

Fish were collected from both the study site and inner Newman Sound using a beach seine. I tagged 33 cod from each of these two locations (66 cod total) and

released them at the same time at the central release point. After 3 hours, each of the patches, the source location, and four control locations were seined. I examined all juvenile Greenland cod for panjet marks and surgical wounds, in addition to VI Alpha tags. Additionally, I recorded the species and length of all animals captured. Large (> 15 cm SL) fish were examined for presence of Floy T-bar tags (see Section 3.2.6). I repeated the mark-release-recapture experiment on three separate days between September 21 and October 26, 2006.

3.2.8 Experimental Design – Flux rate comparison

In the summer of 2007, eelgrass was removed from three sites at Bermuda Beach by divers. Each site consisted of two 9 m by 9 m areas of removal, located 10 m apart (edge to edge), and the sites were separated by at least 100 m (Figures 3.4 and 3.5). The removals were located approximately 20 m from the shoreline at a water depth of 4-5 m. In the centre of each removal, a 5 m^2 patch of artificial eelgrass was affixed to the substrate (see Section 3.2.6). Therefore, at each site two eelgrass patches were separated by approximately 16 m, with a gap between the edge of the eelgrass patches and the surrounding matrix of natural eelgrass habitat. I recorded these patches as BB1a, BB1b, BB2a, BB2b, BB3a, and BB3b (BB – Bermuda Beach, 1, 2 or 3 – site number, a or b – patch identifier), in a south-north orientation. At Big Cold East, 5 m^2 patches of eelgrass were deployed at three sites located at least 40 m apart (Figure 3.6). Each site consisted of two eelgrass patches affixed to the substrate approximately 16 m apart at a water depth of 2 m. This layout created sites designed to mimic the site design at the Bermuda Beach site, however the surrounding matrix was bare substrate instead of natural eelgrass. These patches were recorded BCE1a,

BCE1b, BCE2a, BCE2b, BCE3a, and BCE3b (BCE – Big Cold East; 1, 2 or 3 – site number; a or b – patch identifier), in a south-north orientation.

On each of September 26, 27 and October 2, 2007, I tagged 150 juvenile Atlantic cod and introduced 25 of them into each of three haphazardly chosen habitat patches at each of the two study sites using release cages (see Section 3.2.6). Mean fish lengths (± standard error) for this experiment were 71.9 ± 0.8 mm, 73.2 ± 0.8 mm, and 60.01 ± 1.04 mm (standard length) for the first, second, and third releases, respectively.

Ninety minutes after release cages were deployed (allowing for 1 hour at large), all patches and control locations (area between the two patches of each site) were seined. In addition to collection seines conducted on each of the release days, additional collection seines were conducted on October 3, 4, and 10 in an attempt to increase the number of recaptured fish. All fish captured in the seine were identified and measured, and all cod were examined for tags and injection wounds. Tags could generally be read with the naked eye however, when necessary, a flashlight with blue light emitting diodes (LED) and tinted glasses were used to read the alphanumeric codes. In two cases, tags could not be read with the LED light and glasses, so the fish were killed using a sharp blow to the back of the head and the tags were then removed and read. Surviving tagged fish were re-released at the recapture location.

In addition to seining at the study sites, the bracketing sites at Little Cold East and South Broad Cove were seined every two weeks to monitor for the presence of additional tagged fish. Unlike the sites at Big Cold East and Bermuda Beach, the seines at the bracket sites were deployed from a 6 m boat approximately 55 m offshore and retrieved by two people standing onshore approximately 16 m apart.

These seine hauls sampled 880 m^2 and were intended to increase the likelihood of recapturing tagged fish at the bracket sites.

3.2.9 Data analysis

Low sample size of recaptured cod at the Bermuda Beach site did not permit analysis of the cod movement flux rate experiment. Because Bermuda Beach could not be used for comparison, the Big Cold East data were examined in isolation to create a description of between-patch movement by Atlantic cod in a field context. Instead of separate sites comprised of pairs of patches, the study area was examined as a single site comprised of six patches separated by various distances. All results were analyzed using the proc GENMOD in SAS (Release 9.1). The GENMOD procedure inputs data into a general linear model and calculates p-values for the model in question based on maximum likelihood. I have provided an example of a full model and the results from the GENMOD procedure in Appendix 1. All figures were created in SigmaPlot based on results from the GENMOD procedure.

First, I examined the possibility that recapture success in a given patch depended on factors related to the patch location or the other fish present in the patch. I assigned each seine haul a binomial response depending on whether released fish were recaptured in that haul, and tested several potential explanatory variables (patch location, total number of fish caught (all species), total number of Atlantic cod caught (tagged and untagged), and number of predators). I used a binomial distribution and evaluated each factor separately, because there were insufficient recapture observations to include multiple terms in the models. An alpha level of 0.05 or less was deemed significant. Furthermore, for sites where recaptured fish were present, I

tested models with the number of recaptures as the response variable and separate comparisons of various explanatory variables (patch location within the cove, total number of fish caught, total number of Atlantic cod caught, and number of predators). I used a normal distribution for this analysis and examined all residuals for normality, randomness, independence, and homogeneity.

For the second portion of my analysis I created recapture histories for each fish released. I tested whether recapture (a binomial response variable) was related to the trial number, the release location, or the length of the tagged fish. I then examined the fish that were recaptured in more detail. I tested the effects of several variables (fish length, trial number, and release location) on the distance between release and recapture locations. Once again, I tested each explanatory variable separately and evaluated model significance using an alpha level of 0.05. When the data were not normal, I used a gamma or poisson distribution.

3.3 Results

3.3.1 Effects of between-patch distance

The experiments conducted during 2006 that examined the effects of inter-patch distance on the odds of between-patch movement did not have sufficient recapture success to determine the probabilities of between-patch movement. I therefore provide a qualitative description of the results of this study.

I recaptured a total of two Greenland cod in the first three replicates of the patch distance experiment. These fish were both released into the southern patch of the 20 meter distance pair, one on August 29 and one on August 30, and both were

recaptured after 24 hours at large. One fish was recaptured in an eelgrass patch 70 m south of the release location, the other in an eelgrass patch 125 m northeast of the release location. In the shortened 3 h release trial of this experiment on September 19, 2006, I recaptured two Greenland cod, both after less than 3 hours at large. One fish was recaptured 160 m southwest of the release location and the other was recaptured at the release location; both were captured in hauls from artificial eelgrass patches. No other fish released for any of these replicates were recaptured during these or any later experiments at any location.

3.3.2 Effects of patch size

The experiments conducted during 2006 to examine the effects of patch size on the probability of between-patch movement did not have sufficient recapture success to determine the probability of between-patch movement. Again, I provide a qualitative description of the results of this study.

I recaptured a total of 11 Greenland cod in the three replicates of the patch size experiment. All individuals were recaptured in the same replicate, and in a single 5 m^2 patch, which was located 30 m north of the release location (one of the two patches closest to the release site). In addition to these 11 individuals, 4 additional marked fish from this replicate were recaptured at the study site 11 days following the release, and 2 more were recaptured at the study site 13 days following release. These additional 6 fish were captured in a seine haul designed to collect Big Cold East resident fish for the second and third replicates of this experiment. The seine was pulled into the study site at the base of the cove, and sampled approximately 880 m^2.

Based on this sample area, these fish were recaptured at least 40 m from the site of release however their exact location within the cove cannot be verified.

3.3.3 Flux rate comparison

There were no juvenile Atlantic cod recaptured at the Bermuda Beach site. I recaptured a total of 35 juvenile Atlantic cod over the duration of the study at the Big Cold East site; 7 that were released in the first replicate run, 3 that were released in the second run, and 25 that were released during the third run. Recaptures were usually caught after 1 hour at large; however, fish were recaptured after as long as 6 days at large.

The likelihood of capturing tagged fish in a given patch increased with a higher total number of cod captured in that patch ($\chi^2 = 11.04$; df = 1, n = 26, p = 0.0009). The probability of capturing tagged Atlantic cod in a given patch was unaffected by the location of the patch ($\chi^2 = 10.20$; df = 8, n = 26, p = 0.2511), the total number of fish in the patch ($\chi^2 = 3.32$; df = 1, n = 26, p = 0.0684), or the number of predators in the patch ($\chi^2 = 2.56$; df = 1, n = 26, p = 0.1094). Analysis of number of recaptures in each patch shows that the number of recaptures in a given patch was unaffected by its location relative to other patches ($\chi^2 = 10.19$; df = 8, n = 26, p = 0.2519) and the total number of predators in the patch ($\chi^2 = 0.73$; df = 1, n = 26, p = 0.3913). However, the number of tagged fish recaptured in a given patch increased as both the total number of Atlantic cod ($\chi^2 = 48.16$; df = 1, n = 26, $p < 0.0001$; Figure 3.7) and the total number of fish in the patch increased ($\chi^2 = 31.92$; df = 1, n = 26, $p < 0.0001$; Figure 3.8).

Analysis of the recapture histories for individual fish show a significant effect of replicate number on the likelihood of any individual fish being recaptured (χ^2 = 24.57; df = 1, n = 224, $p < 0.0001$). Over 68% (24/35) of the recaptured fish were recaptured in the third replicate. Smaller fish were more likely to be recaptured than larger fish ($\chi^2 = 11.52$; df = 1, n = 224, $p = 0.0007$). Release location had no effect on the probability of a fish being recaptured ($\chi^2 = 6.19$; df = 1, n = 224, $p = 0.2883$). Larger recaptured fish were recaptured further from the release point than were smaller recaptured fish ($\chi^2 = 6.54$; df = 1, n = 31, $p = 0.0105$; Figure 3.9). There were also significant differences between the average distance travelled by recaptured fish released at different locations ($\chi^2 = 28.27$; df = 5, n = 31, $p < 0.0001$; Figure 3.10). Fish released at the most southerly patch (closest to the base of the cove) travelled further than fish released at other locations.

3.4 Discussion

3.4.1 Between-patch distance and patch size experiments

These two experiments resulted in very low recapture rates for Greenland cod, and highlight the lack on knowledge about movement rates at this stage of their development. Given the increased predation risk of leaving complex habitat (Linehan et al. 2001, Laurel et al. 2003b), my expectations at the beginning of this study had been that juvenile cod would tend to remain in the eelgrass patches and the likelihood of movement would decrease as between-patch distance increased. Similarly, I expected that juvenile fish that did migrate would be more likely to move to larger

patches of eelgrass than smaller ones as a result of the decrease in predation risk associated with larger patch size (Laurel et al. 2003b).

Previous work indicates that juvenile cod move on scales of hundreds of meters (Tupper and Boutilier 1995, Sheppard 2005), and it was on this basis that I selected a study area approximately 2.5 km^2 in size. I expected that this area would be sufficient to encompass movement of juvenile cod for periods of at least several days, and allow sufficient spatial sampling intensity to recapture tagged fish. In 2006, recruitment of juvenile Atlantic cod was low compared to previous years (Gregory et al. 2006, pers. obs.), resulting in low availability of fish for tagging. For this reason, juvenile Greenland cod were used instead of Atlantic cod. The results of both of these experiments suggest that juvenile Greenland cod move at scales larger than hundreds of meters, and over time periods of 24 hours or less. This finding agrees with Laurel et al. (2004), which suggests movement scales of kilometres over short time periods. Another explanation for the low recapture rates could be that the high mobility of juvenile cod within my study site precluded recapture of marked fish despite the high sampling intensity. Despite the low number of recaptures, it should be noted that my recapture rates for these experiments (approximately 2 percent and 8 percent for the distance and patch size experiments, respectively) were comparable to those of Laurel et al. (2004), where recapture rates of approximately 3 percent were observed. Laurel et al. (2004) suggested that juvenile cod outside of complex habitat aggregate and move quickly over open areas. If this occurred during my two experiments, it is possible that the artificial eelgrass patches I provided did not offer sufficient cover to offset the barren substrate of the study area and fish subsequently moved elsewhere. It

was with this possibility in mind that I designed the second experiment in which I expanded the size of two of the experimental patches; however, recapture success in these patches did not increase, suggesting that juvenile Greenland cod may assess the suitability of eelgrass habitat at scales of hundreds or thousands of square meters. It is unknown how far juvenile cod are capable of seeing; research on the response of juvenile Atlantic cod to mysid prey shows a response to visual cues at a distance of approximately 30 cm (Meager et al. 2005) and it is probable that cod have visual contrast thresholds comparable to humans (Anthony 1981). It is possible that fish released during this or the flux rate comparison study could not see the eelgrass patches placed within the study area, but this is not known with any degree of certainty. Finally, as with any behavioural study, it is possible that disturbance from the experiment itself may have affected fish behaviour. Where possible, measures were taken to minimize such disturbance (remote release mechanisms on the cages to minimize flight response), and established experimental procedures (i.e. tagging and seining protocols) were used at all times.

3.4.2 Flux rate comparison

I conducted my flux rate experiment with the expectation that recapture rates at the eelgrass matrix site (Bermuda Beach) would be higher than that of the Big Cold East site. I based this expectation on the results of the previous two experiments which, though conducted on Greenland cod, suggested that movement of gadids at the Big Cold East site was likely to be high. Additionally, work by Sheppard (2005) suggested that movement rates in continuous eelgrass habitat were on the scale of hundreds of meters. The Bermuda Beach site was designed so that pairs of patches

were separated by at least 100 meters, therefore the entire study area extended along approximately 400 meters of coastline. Finally, Laurel et al. (2004) found that juvenile cod dispersed did not reflect a simple diffusive pattern, and the majority of the recaptures in that study occurred during the early part of the experiment. It was for this reason that the time at large before the first recapture attempt was shortened to one hour, and based on the large amount of suitable protective habitat in the study area at Bermuda Beach, I did not expect fish to travel far because suitable habitat was readily available. Contrary to expectations, there were no recaptures at the Bermuda Beach site at any time during the experiment. I believe that this may have resulted from the widespread availability of protective habitat in the area, which was likely to decrease the risk of emigration from the study area. Furthermore, the Bermuda Beach location was very exposed to prevailing winds, and few fish of any species were caught in seines at that location suggesting that, despite the large amount of available natural eelgrass habitat, the site was not ideally suited to juvenile fish. This result was unexpected, given that the site had been used previously for mark-recapture experiments (Laurel et al. 2004) and has been used as a collection site for juvenile cod for multiple years prior to my use of the area, and generally yielded high catch rates of fish (for Laurel et al. 2004, approximately 2000 fish were captured, batch marked, and released at the Bermuda beach site). Finally, this low capture rate was unexpected given that 2007 was a year of very high recruitment for juvenile Atlantic cod (pers. obs.). Based on Laurel et al. (2004), I had expected that a site with large eelgrass cover in a year of high fish density would be strongly utilized by juvenile fish communities. Instead, the Big Cold East site, despite a landscape of barren

substrate interrupted only by the artificial eelgrass patches, regularly yielded tens to hundreds of fish of varying species composition in seine hauls.

Nonetheless, the recapture data from Big Cold East does allow me to draw several inferences about the behaviour of juvenile Atlantic cod in fragmented habitat. My results show that areas with larger numbers of fish were more likely to include tagged fish. This result is intuitive, but also speaks to the aggregative nature of juvenile cod. Laurel et al. (2004) showed that juvenile Atlantic cod aggregate over open areas, and several species have been shown to aggregate to reduce the risk of predation (Cresswell 1994, Foster and Treherne 1981, Krebs and Davies 1991). I showed in Chapter 2 that group size may affect movement behaviour in the presence of predators. Based on the fish assemblage captured in the seine hauls at the Big Cold East site, there were predatory species present, and it is reasonable to surmise that the released fish would aggregate to minimize predation risk. By analyzing the data from recaptured fish, I have shown that larger fish were recaptured at greater distances from their release location. This result was not unexpected given the increased swimming capabilities of larger fish compared to their smaller counterparts. This result may also be due to the reduced predation risk for larger fish (Sogard 1997) that may result in increased willingness to move outside of protective habitat.

3.4.3 Implications and Conclusions

I have demonstrated that movement out of an area of fragmented habitat appears to be high, but that additional work is required to quantify the impacts of fragmented habitat on juvenile fish. Despite the extensive eelgrass at the Bermuda Beach site, I captured few fish there, suggesting that further research is necessary to

determine what other factors affect the suitability of habitat for juvenile Atlantic cod. Furthermore, I determined that the presence of conspecifics plays a large part in the response of juvenile cod to habitat fragmentation. Further tagging and tracking studies are needed to determine how conspecific group size might interact with the degree of fragmentation to affect movement between patches. Finally, I found that larger fish appear to move further than smaller fish, a finding which should be further examined to determine the periods when juvenile fish are most vulnerable to habitat fragmentation. Habitat fragmentation can occur through both natural and anthropogenic means. My study has shown that there are a variety of factors that determine how juvenile fish respond to such fragmentation, and indicates that further work is needed to elucidate the exact nature of such responses.

3.5 References

Anthony, P.D. 1981. Visual contrast thresholds in the cod *Gadus morhua L.* Journal of Fish Biology 19: 87-103.

Baker, L. 2007. Effects of corridors on the movement behaviour of the jumping spider *Phidippus princeps* (Araneae Salticidae). Canadian Journal of Zoology 85: 802-808.

Beier, P. 1993. Determining minimum habitat areas and habitat corridors for cougars. Conservation Biology 7: 94-108.

Cote, D., Moulton, S., Frampton, P.C.B., Scuton, D.A., McKinley, R.S. 2004. Habitat use and early winter movements by juvenile Atlantic cod in a coastal area of Newfoundland. Journal of Fish Biology 64: 665-679.

Creegan, H.P., Osborne, P.E. 2005. Gap-crossing decisions of woodland songbirds in Scotland: an experimental approach. Journal of Applied Ecology 42: 678-687.

Cresswell, W. 1994. Flocking is an effective anti-predation strategy in redshanks, *Tringa tetanus*. Animal Behaviour 47: 433-442.

Dalley, E.L., Anderson, J.T. 1997. Age-dependent distribution of demersal juvenile Atlantic cod (*Gadus morhua*) in inshore/offshore northeast Newfoundland. Canadian Journal of Fisheries and Aquatic Sciences 54 (Suppl. 1): 168-176.

deYoung, B., Rose, G.A. 1993. On recruitment and distribution of Atlantic cod *(Gadus morhua)* off Newfoundland. Canadian Journal of Fisheries and Aquatic Sciences 50: 2729-2741.

Ennis, G.P. 1970. Reproduction and associated behaviour in shorthorn sculpin, *Myoxocephalus scorpius* in Newfoundland waters. Journal of the Fisheries Research Board of Canada 27: 2037-2045.

Foster, W.A., Treherne, J.E. 1981. Evidence for the dilution effect in the selfish herd from fish predation in a marine insect. Nature 295: 466-467.

Gotceitas, V., Fraser, S., Brown, J.A. 1997. Use of eelgrass beds (*Zostera marina*) by juvenile Atlantic cod (*Gadus morhua*). Canadian Journal of Fisheries and Aquatic Sciences 54: 1306-1319

Grant, S.M., Brown, J.A. 1997. Nearshore settlement and localized populations of Age 0 Atlantic cod (*Gadus morhua*) in shallow coastal waters of Newfoundland. Canadian Journal of Fisheries and Aquatic Sciences 55: 1317-1327.

Gregory, R.S., Methven, D.A., Wheeler, L.A., Schneider D.C., Brown, J.A. 2000. Relative strength of the 1999 year-class, from nearshore surveys of demersal age 0 Atlantic cod in 3KL and in Newman Sound, Bonavista Bay. Canadian Stock Assessment Secretariat Research Document. 2000/094.

Gregory, R.S., C. Morris, G.L. Sheppard, M.E. Thistle, J.E. Linehan, and D.C. Schneider. 2006. Relative strength of the 2003 and 2004 year-classes, from nearshore surveys of demersal age 0 & 1 Atlantic cod in Newman Sound, Bonavista Bay. Canadian Science Advisory Secretariat Research Document. 2006/038.

Hutchings, J.A., Myers, R.A. 1994. What can be learned from the collapse of a renewable resource? Atlantic cod, *Gadus morhua*, of Newfoundland and Labrador. Canadian Journal of Fisheries and Aquatic Sciences 51: 2126-2146.

Hutchings, J.A., Myers, R.A., Lilly, G.R. 1993. Geographic variation in the spawning of Atlantic cod, *Gadus morhua*, in the Northwest Atlantic. Canadian Journal of Fisheries and Aquatic Sciences 50: 2457-2467.

Krebs, J.R., Davies, N.B. 1991. Behavioral Ecology 3rd Edn. Blackwell Scientific. Boston.

Laurel, B.J., Gregory, R.S., Brown, J.A. 2003 (a). Settlement and distribution of Age-0 juvenile cod, *Gadus morhua* and *G. ogac*, following a large-scale habitat manipulation. Marine Ecology Progress Series 262: 241-252.

Laurel, B.J., Gregory, R. S., Brown, J.A. 2003 (b). Predator distribution and habitat patch area determine predation rates on age-0 Atlantic cod, *Gadus spp*. Marine Ecology Progress Series 251: 245-254.

Laurel, B.J., Gregory, R.S., Brown, J.A., Hancock, J.K., Schneider, D.C. 2004. Behavioural consequences of density-dependent habitat use in juvenile cod *Gadus morhua* and *G. ogac*: the role of movement and aggregation. Marine Ecology Progress Series 272: 257-270.

Lear, W.H., Fleming, A.M., Wells, R. 1980. Results of small cod surveys in eastern Newfoundland during 1959-64. NAFO SCR Document 80/144.

Linehan, J.E., Gregory, R.S., Schneider, D.C. 2001. Predation risk of age-0 cod (*Gadus*) relative to depth and substrate in coastal waters. Journal of Experimental Marine Biology and Ecology 263: 25-44.

Luksenburg, J.A., Pedersen, T. 2002. Sexual and geographic variation in life history parameters of the shorthorn sculpin. Journal of Fish Biology 61: 1453-1464.

Meager, J.J., Solbakken, T., Utne-Palm, A.C., Oen, T. 2005. Effects of turbidity on the reactive distance, search time and foraging success of juvenile Atlantic cod (*Gadus morhua*). Canadian Journal of Fisheries and Aquatic Sciences 62: 1978-1984.

Methven, D.A., Schneider, D.C. 1998. Gear-independent patterns in variation of catch in juvenile Atlantic cod (*Gadus morhua*) in coastal habitat. Canadian Journal of Fisheries and Aquatic Sciences 55(6): 1430-1442.

Morris, C.J., Green, J.M. 2002. Biological characteristics of a resident population of Atlantic cod (*Gadus morhua*) in southern Labrador. ICES Journal of Marine Science 59: 666-678.

Orth, R.J., Heck, K.L., van Montfrans J. 1984. Faunal communities in seagrass beds: A review of the influence of plant structure and prey characteristics on predator: prey relationships. Estuaries 7: 339-350.

Robbins B.D., Bell, S.S. 1994. Seagrass landscapes: a terrestrial approach to the marine subtidal environment. Trends in Ecology and Evolution 9: 301-304.

Ruzzante, D.E., Wroblewski J.S., Taggart, C.T., Smedbol, R.K., Cook, D., Goddard, S.V. 2000. Bay-scale population structure in coastal Atlantic cod in Labrador and Newfoundland, Canada. Journal of Fish Biology 56: 431-447.

Scott, W.B., Scott, M.G. 1988. Atlantic Fishes of Canada. Canadian Bulletin of Fisheies and Aquatic Sciences 219: 713 pp.

Sheppard, G.L. 2005. Natural mortality and movement of juvenile cod (*Gadus spp.*) inhabiting eelgrass (*Zostera marina*) in coastal Newfoundland waters. MSc Thesis, Department of Biology, Memorial University of Newfoundland.

Sogard, S.M. 1997. Size-selective mortality in the juvenile stage of teleost fishes: a review. Bulletin of Marine Science 60: 1129-1157.

Sogard, S.M., Olla, B.L. 1993. The influence of predator presence on utilization of artificial seagrass habitats by juvenile walleye pollock, *Theragra chalcogramma*. Environmental Biology of Fishes 37: 57-65

Stokesbury, M.J.W., Cosgrove, R., Boustany, A., Browne, D., Teo, S.L.H., O'Dor, R.K., Block, B.A. 2007. Results of Satellite tagging of Atlantic bluefin tuna, *Thunnus thynnus*, off the coast of Ireland. Hydrobiologia 582: 91-97.

Tanaka, Y., Mohri, M., Yamada, H. 2007. Distribution, growth and hatch date of juvenile Pacific bluefin tuna *Thunnus orientalis* in the coastal area of the Sea of Japan. Fisheries Science 73: 534-542.

Templeman, W. 1979. Migration and intermingling of stocks of Atlantic cod, *Gadus morhua*, of the Newfoundland and adjacent areas from tagging in 1962-66. ICNAF. Research Bulletin 14: 5-50.

Tupper, M., Boutilier, R.G. 1995. Size and priority at settlement determine growth and competitive success of newly settled Atlantic cod. Marine Ecology Progress Series 118: 295-300.

Wroblewski, J.S., Bailey, W.L., Howse, K. A. 1994. Observations of adult Atlantic cod (*Gadus morhua*) overwintering in nearshore waters of Trinity bay, Newfoundland. Canadian Journal of Fisheries and Aquatic Sciences 51: 142-150.

Wroblewski, J.S., Hiscock, H.W. 2002. Enhancing the reproductive potential of local populations of coastal Atlantic cod (*Gadus morhua*). Canadian Journal of Fisheries and Aquatic Sciences 59: 1685-1695.

Zollner, P.A., Lima, S.L. 1999. Illumination and the perception of remote habitat patches by white-footed mice. Animal Behaviour 58: 489-500.

Figure 3.1: Location of study sites for field experiments conducted in 2006 and 2007

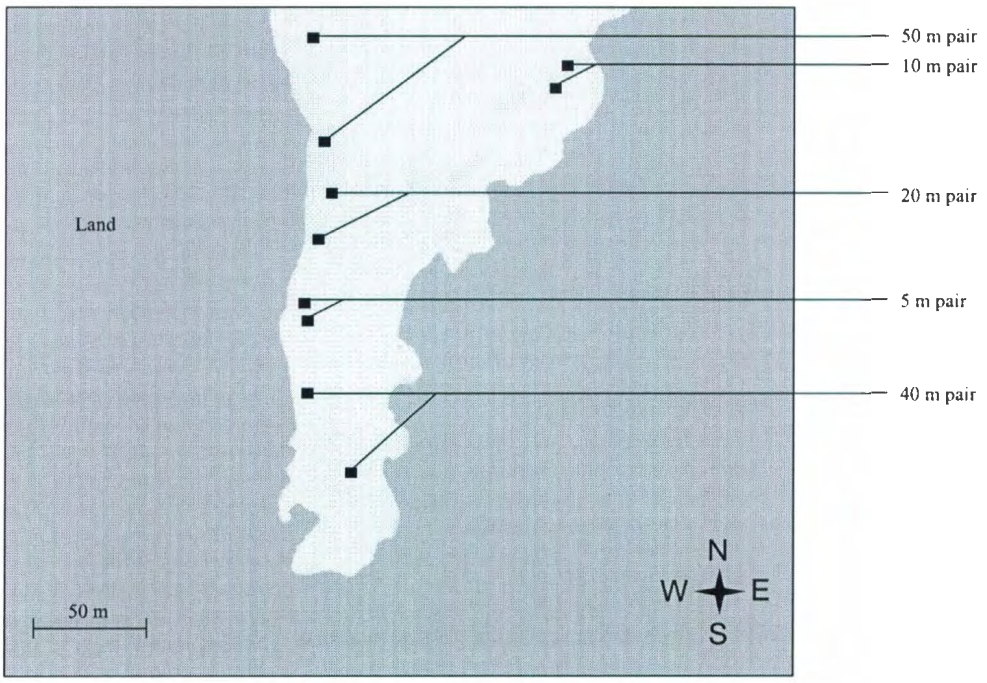

Figure 3.2: Patch locations for between-patch distance experiment at Big Cold East (48° 34' N, 53° 49' W), August 28 – September 19, 2006. Between-patch distances for each pair are noted above

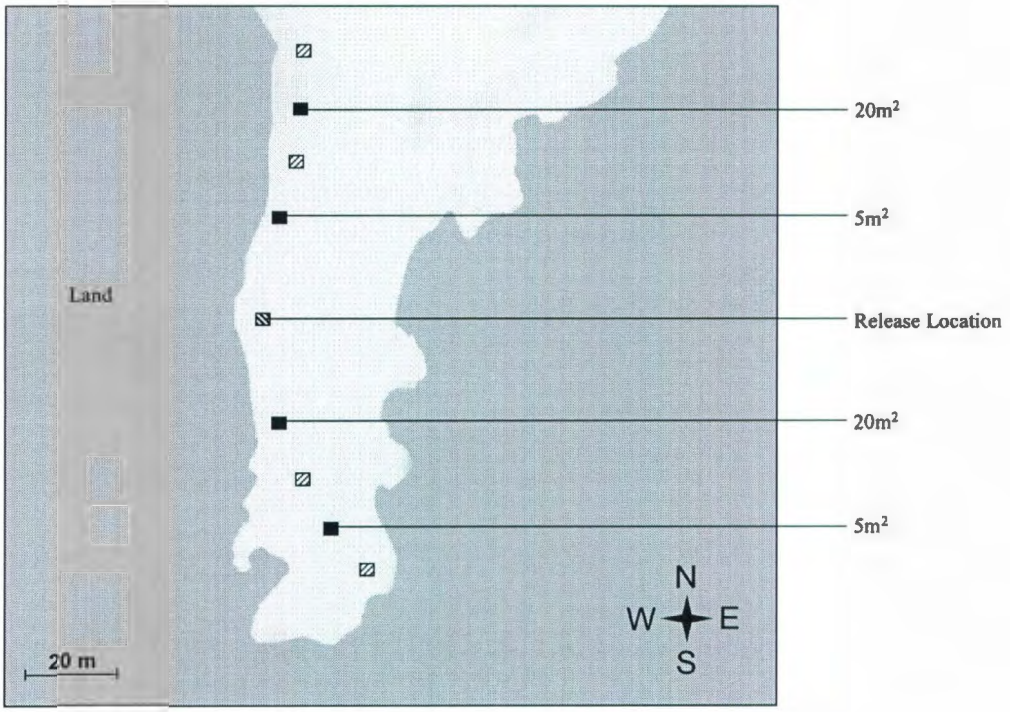

Figure 3.3: Patch configuration for patch size experiment at Big Cold East (48° 34' N, 53° 49' W), September 21 – October 26, 2006. Patches are indicated by solid black boxes, with areas noted above, and control locations are indicated by hatched boxes

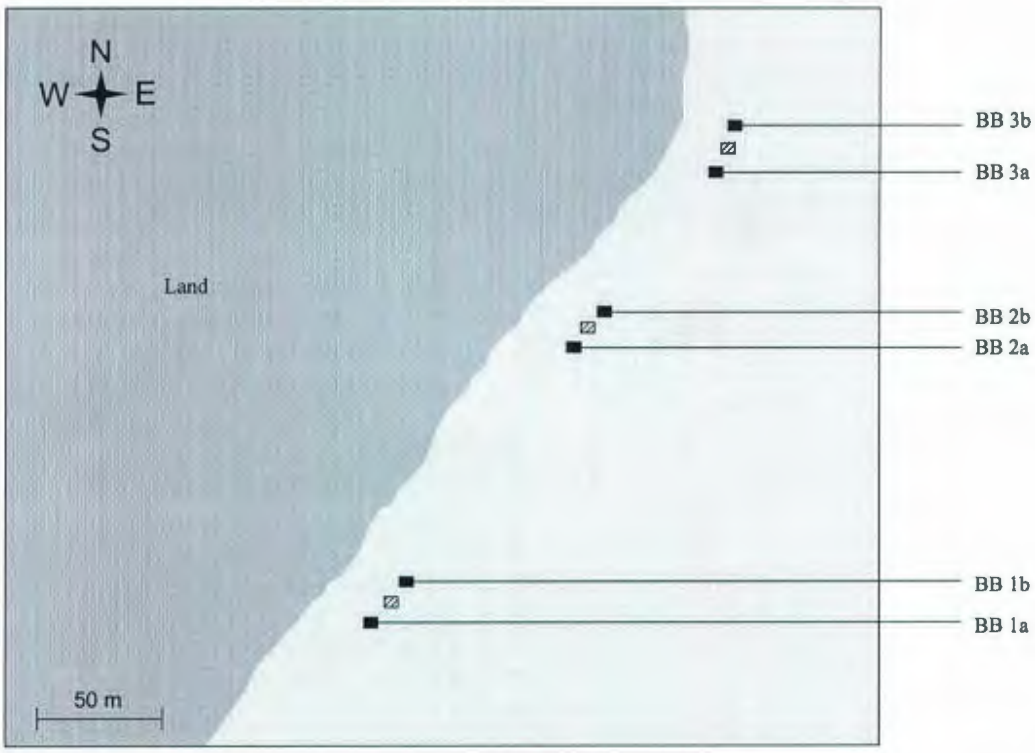

Figure 3.4: Site configuration for eelgrass removals at Bermuda Beach (48° 35' N, 53° 55' W) during the flux rate comparison study from September 26 – October 2, 2007. Patch locations are indicated by solid black boxes with patch identifiers noted above and control locations are indicated by hatched boxes

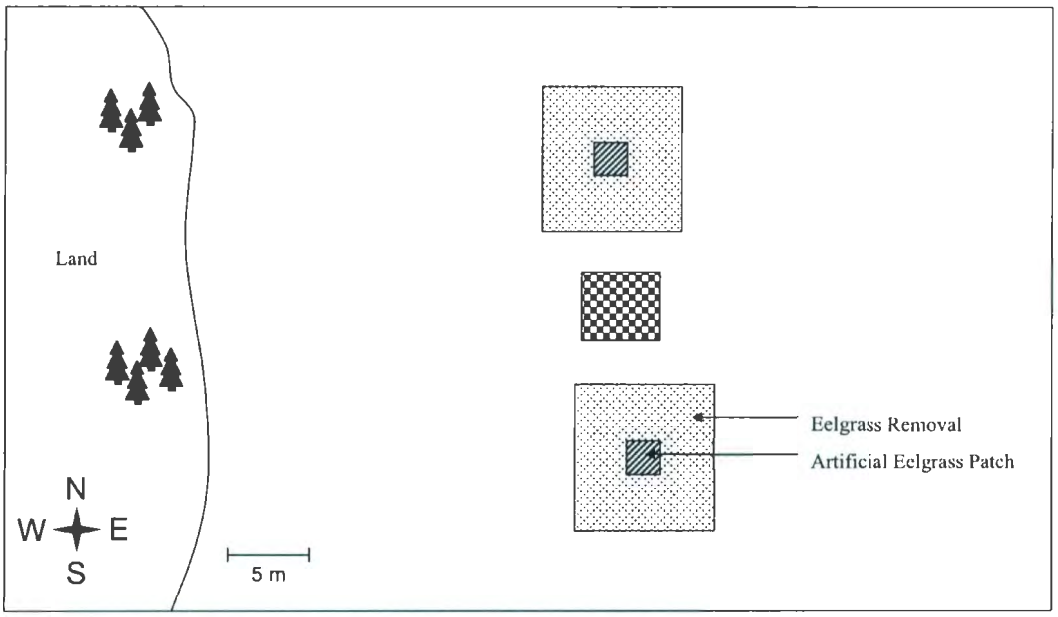

Figure 3.5: Configuration of each pair of eelgrass removals and patch placements at the Bermuda Beach site (48° 35' N, 53° 55' W) during the flux rate comparison study from September 26 – October 2, 2007 with the control location indicated by a checked box

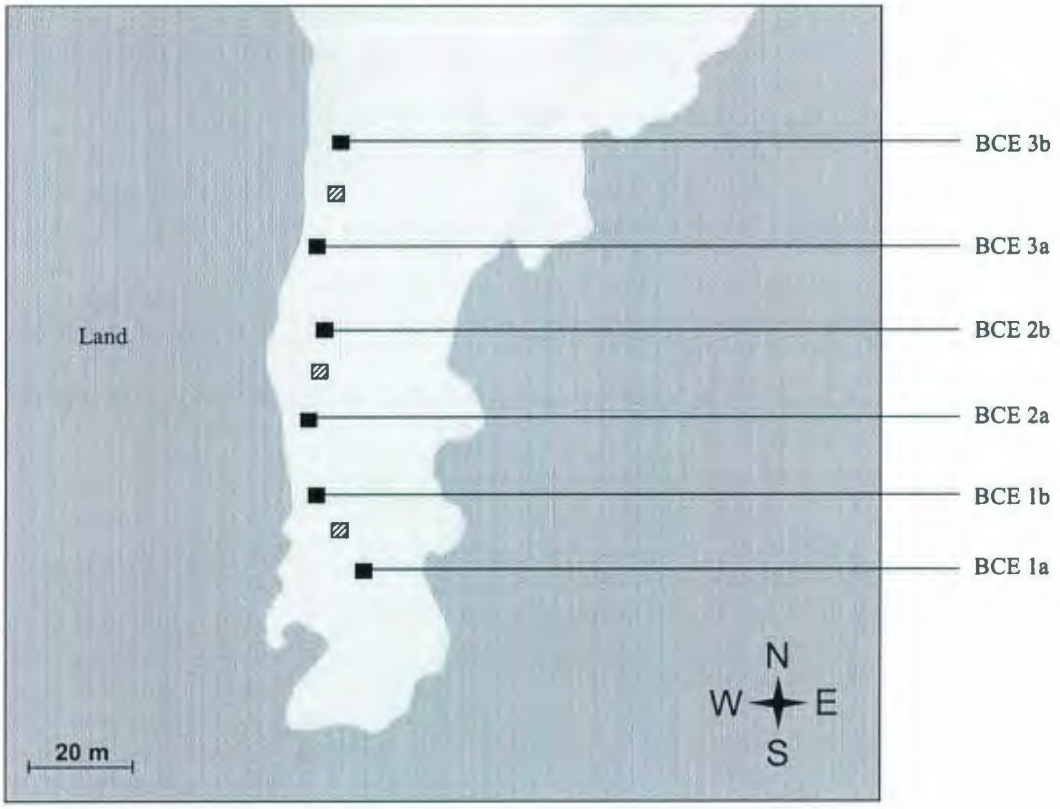

Figure 3.6: Configuration of patches and control sites at Big Cold East (48° 34' N, 53° 49' W), during the flux rate comparison study from September 26 – October 2, 2007 . Eelgrass patches are indicated by solid black with patch identifiers noted above and control locations are indicated by hatched boxes

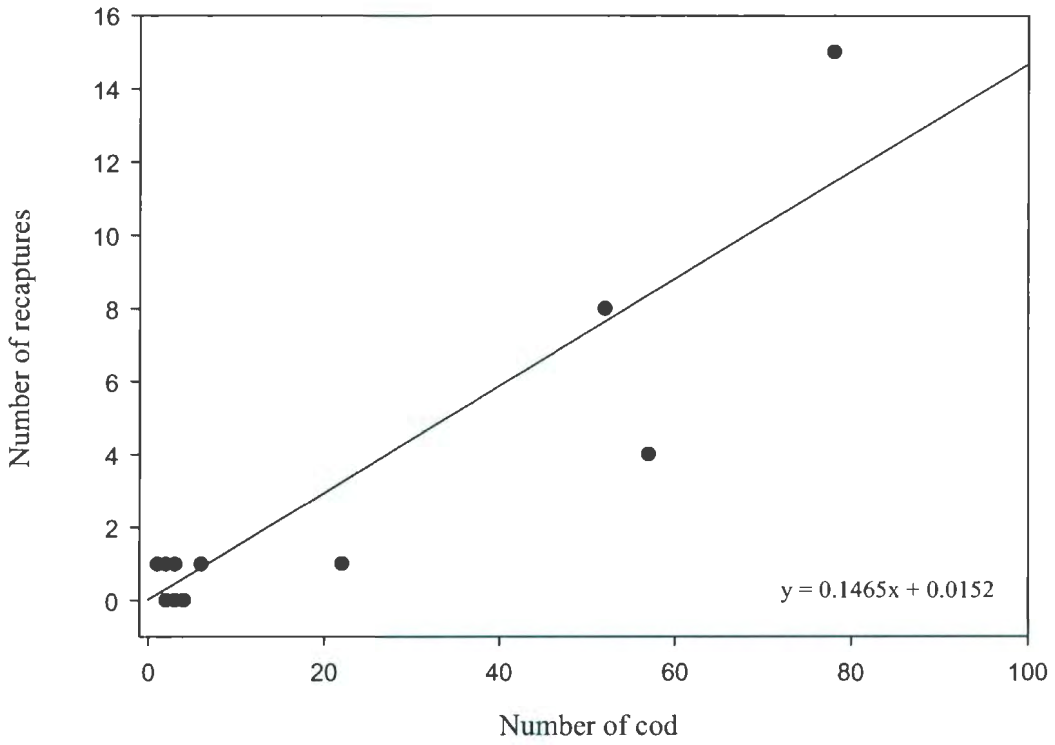

Figure 3.7: Number of recaptures regressed against the number of cod in a patch at Big Cold East during the flux rate comparison study from September 26 – October 2, 2007 (only includes patches where cod were caught)

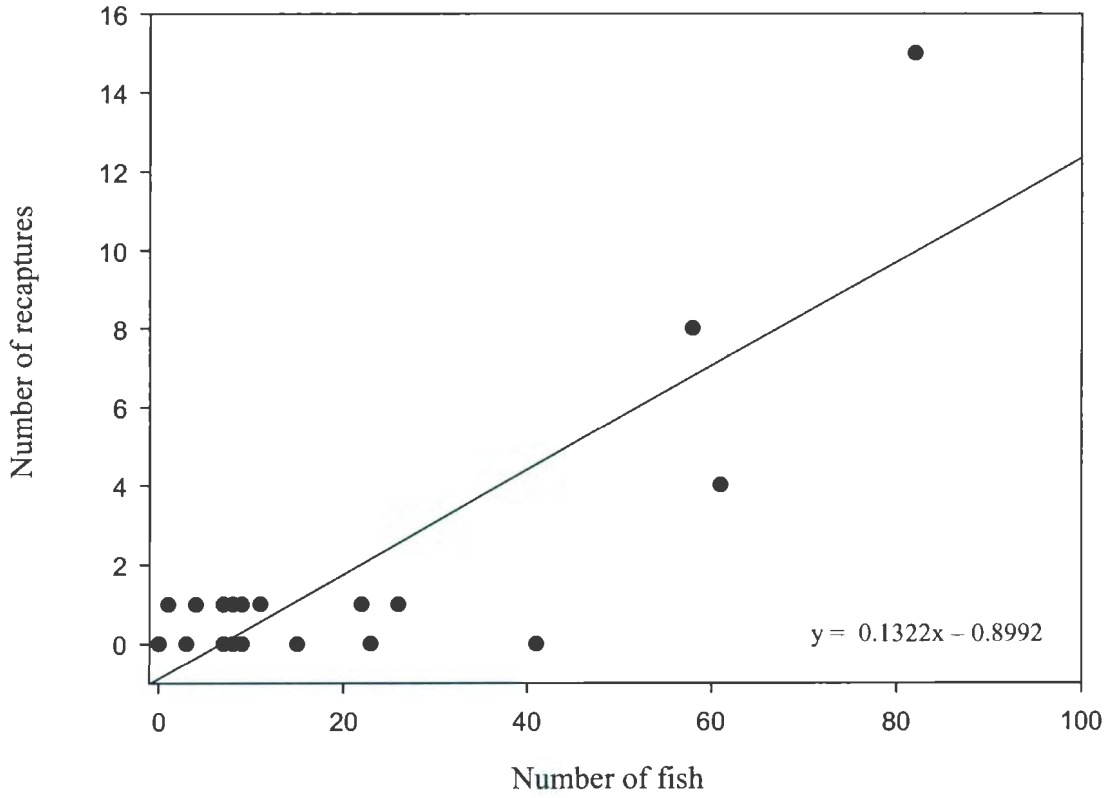

Figure 3.8: Number of recaptured cod regressed against the total number of fish in a patch at Big Cold East during the flux rate comparison study from September 26 – October 2, 2007 (includes all patches)

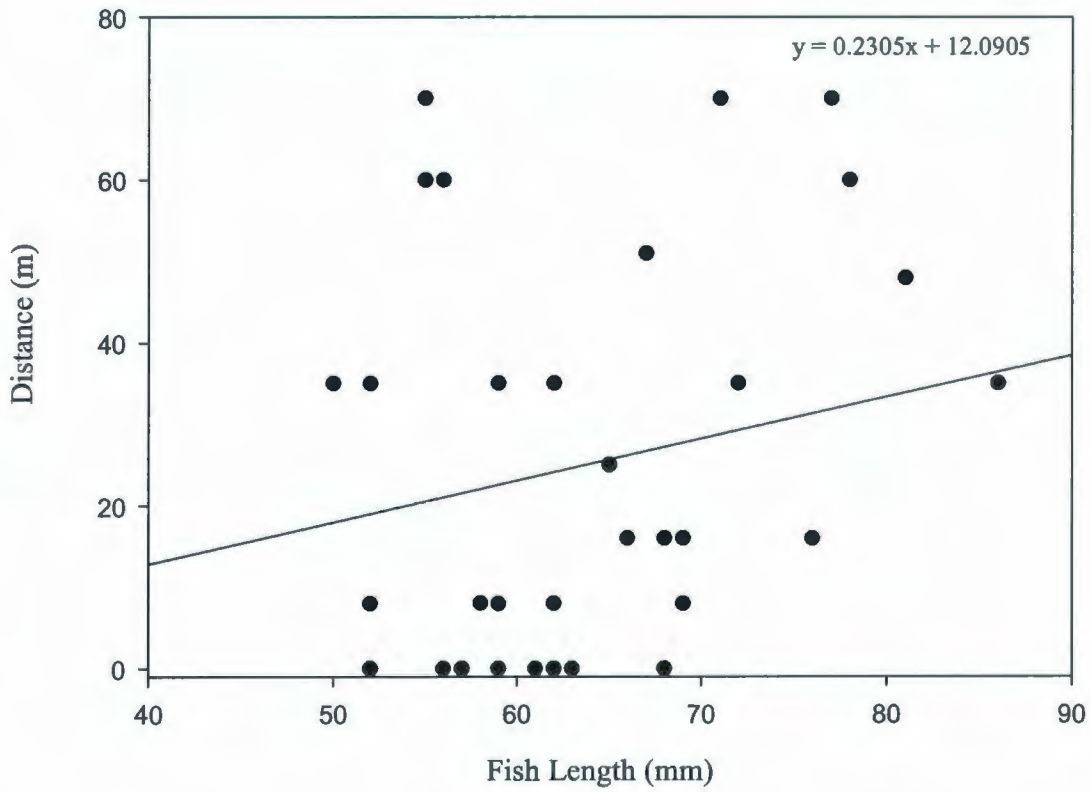

Figure 3.9: Distance between release location and recapture location regressed against fish length (SL) for all recaptured fish at Big Cold East during the flux rate comparison study from September 26 – October 2, 2007

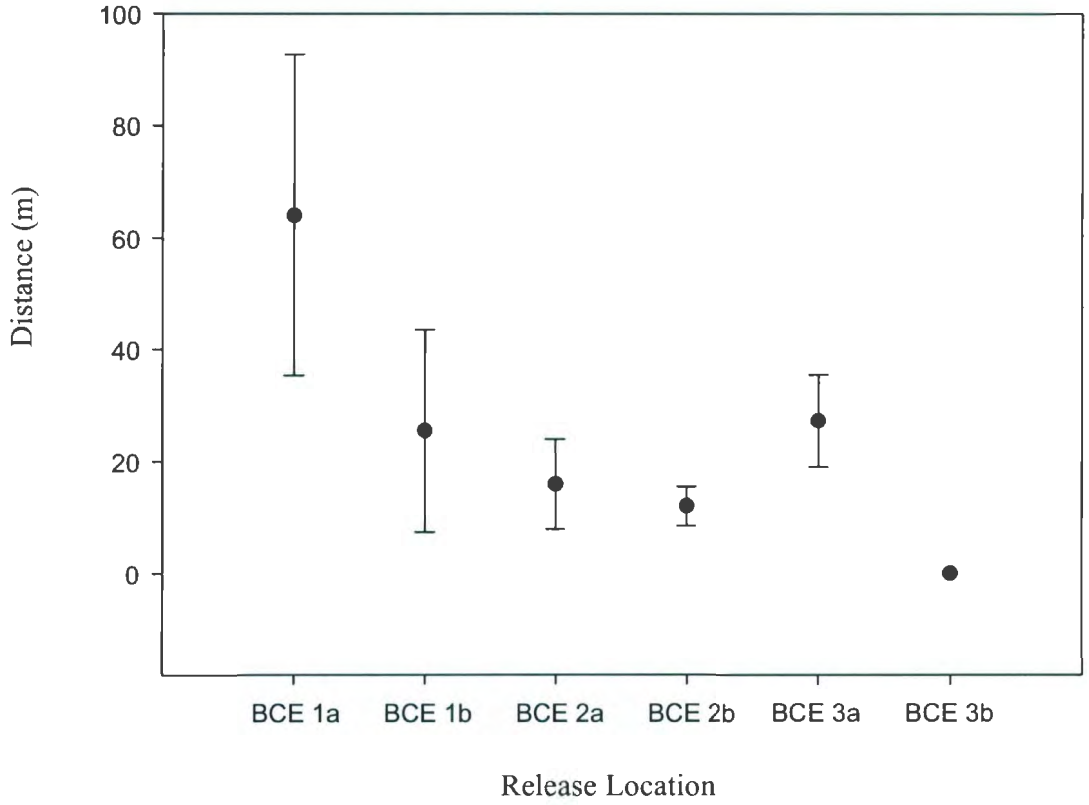

Figure 3.10: Distance between release and recapture locations (± SE) for recaptured juvenile Atlantic cod released at various locations at Big Cold East during the flux rate comparison study from September 26 – October 2, 2007

Chapter 4: Summary, Conclusions and Further Work

In my thesis, I have presented complementary laboratory and field experiments that examined the movement of juvenile Atlantic cod in highly fragmented habitat. I have demonstrated that the movement of juvenile Atlantic cod between patches of protective habitat is mediated by several factors that include distance between patches, predator presence, group size, and fish length. Additionally, I have shown that juvenile cod movement rates in an area of fragmented habitat in the field are difficult to quantify, but appear to be high. Moreover, I have illustrated that concepts used in terrestrial landscape ecology can be applied to marine systems, and marine animals can exhibit movement patterns similar to those of terrestrial species when faced with fragmented habitat. I also have added to the body of evidence showing that gaps in habitat may create a barrier to dispersal for animals that associate with physically complex habitat. In this thesis, I have addressed several aspects of animal-habitat associations including predator-prey interactions, habitat complexity, habitat fragmentation, and movement behaviour.

The association between animals and complex habitat has been studied in multiple species ranging from birds and mammals to fish and crustaceans. This association appears to be driven by reduced predation risk in areas of physically complex habitat (Rood 1972, Lima et al. 1987, Lima 1990, Tupper and Boutilier 1997, Kopp 2006). Although previous studies have examined the effect of this differential predation risk on the movement behaviour of several species, most of this work has focussed on terrestrial species (Zollner and Lima 1990, Desrochers and Hannon 1997, Bright 1998, Bosschieter and Goedhart 2005). No studies have

explicitly looked at movement behaviour of marine species as they navigate fragmented habitat. My research addressed this component of animal behaviour by using laboratory experiments to determine factors that mediate between-patch movement behaviour of Atlantic cod, and complementary field studies to examine between-patch movement behaviour in a natural setting.

This approach allowed me to complete the first examination of the factors that affect between-patch movement of juvenile cod and describe this movement in a natural environment. Laboratory studies make it possible to constrain the number of potential variables that influence animal decisions, therefore allowing researchers to isolate different components of animal behaviour. Laboratory conditions are, however, unnatural environments for test subjects by definition, and cannot reflect the full spectrum of factors that animals in the wild navigate on a daily basis. It is therefore always a concern that laboratory experiments only reflect one component of animal behaviour, and that results may be an artefact of the laboratory conditions (see Magurran et al. 1996). Conversely, field experiments allow researchers to examine animals in the most natural conditions possible, and behavioural observations made in a natural setting are likely to be the most valid in terms of being free from experimental artefact (assuming the experiments or observations themselves are minimally disruptive to the animal). However, field experiments are subject to numerous uncontrolled and unknown variables, leading to results that may be difficult to attribute to any particular variable. This trade-off between the empirical strength of lab studies and the reality of behavioural decisions in the wild has long been a subject of debate in the scientific community and a challenge in the design of behavioural

experiments. The research I report on in my thesis tackled both aspects of this division, by first examining individual factors that affect between-patch movement in the lab, and second, completing a study of between-patch movement behaviour in the field. By examining the results of these studies in concert it is possible to gain a more complete picture of the movement behaviour of juvenile Atlantic cod and verify aspects of the lab work in the field. Collectively, this work provides insight into the potential impacts of habitat destruction on this species.

My laboratory work (Chapter 2) identified several factors that affect between-patch movement behaviour of juvenile Atlantic cod. I determined that predator presence and increased between-patch distance both caused a decrease in between-patch movement frequency. This reluctance to cross open areas is mirrored by terrestrial species in their responses to gaps (Desrochers and Hannon 1997, Bright 1998, Baker 2007) and suggests that habitat gaps may act as a movement barrier for marine species. I also identified group size as a factor that modified the response of Atlantic cod confronted with highly fragmented habitat. Fish that associated with larger numbers of conspecifics moved between patches more frequently, suggesting that conspecifics mitigate the risk of moving in open areas. This research supports the literature on both terrestrial and marine species that suggests a reduction in perceived risk for animals in larger groups of conspecifics (i.e. flocks of birds, schools of fish, and herds of ungulates). These results provide information on the various factors that influence the movement of juvenile Atlantic cod outside areas of protective habitat. However, within a natural context I was unable to determine exactly how they react to highly fragmented habitat.

My field experiments (Chapter 3) were designed to investigate the movement rate of juvenile Atlantic cod in an area of highly fragmented habitat in the wild. Previous movement studies of juvenile Atlantic cod have been conducted in areas of continuous eelgrass, and showed high movement rates in such areas. Originally, I had expected that in highly fragmented habitat, movement rates would be lower and fish would remain in the available habitat rather than risking movement over open areas to reach other habitat. In the first year of my field work, extremely low recapture success within the study site indicated that this hypothesis was incorrect. Based on the information gained in the first year of my study, I modified my field work in the second year to compare movement between patches in a matrix of eelgrass and movement in a matrix of barren habitat. The low recapture success in the second set of experiments highlights the difficulties of applying terrestrial techniques to marine systems; instead of visually tracking animals, such as birds, as they move through open areas, movement of small fish can only be determined through knowledge of their release and recapture points; detailed information about the path taken by the fish is not readily obtained. Such information can be determined using Passive Integrated Transponder (PIT) tags or sonar tags and networks of receivers (Cote et al. 2004, Barry et al. 2007, Ng et al. 2007); however, setting up sufficient receiver networks is logistically challenging. Additionally, without direct control over the majority of experimental conditions (temperature, predator density and distribution, conspecific density distribution, substrate composition, etc.), it was impossible to determine the reason for low recapture success.

Despite these difficulties, some inferences can be drawn from the fish that were recaptured over the course of my field studies. Primarily, juvenile cod appeared to move quickly out of areas of highly fragmented habitat, as demonstrated by the extremely low recapture success over longer time scales in the flux rate comparison study. This finding suggests that highly fragmented habitat is unsuitable for juvenile Atlantic cod, and is also one which is supported by previous work on foraging and predation trade-offs (Thistle 2006). In addition, my data suggest that fish were aggregating within the study area, once again suggesting that movement for fish may be affected by the number of conspecifics in a group. I also found that fish length affected the distance between release and recapture points, with larger fish being captured at further distance from their release location and larger fish being less likely to be recaptured at all.

The results of the field and lab experiments can be considered together to gain a more complete picture of juvenile Atlantic cod movement. Fish length was a significant factor in both the field and lab studies, further lending support to the "bigger is better" hypothesis (see Sogard 1997), and indicating that fish may assess risky situations differently based on their size. Both of my studies suggest that larger fish move faster in open areas; fish in the laboratory experiment moved faster between patches and fish in my field experiment moved quickly out of the study area. Furthermore, my lab results showed that fish move more quickly in open areas when the travel distance to the next habitat patch is larger. This result may have been partially supported by the field studies, in that the results suggest that, presented with a field matrix of patches separated by large distances in an area with little other cover,

fish moved quickly out of the study area. The nearest natural eelgrass to the study area was approximately 500 m from the head of the cove, creating very large distance to the nearest optimal habitat. In addition to these results, some similarities between the field and lab work can also be seen when examining the effects of group size and predator relationships. In the field, I was able to determine that large numbers of predators were present in the study area, suggesting that aggregation would be a likely response by the released juvenile fish. This hypothesis appeared to be supported by the apparent aggregation of the recaptured fish in the field study. Additionally, during the laboratory experiments with the predator present, fish that associated with larger numbers of conspecifics moved more quickly over open areas than did those associating with fewer conspecifics. When comparing this result to the field experiments, it would be reasonable to surmise that fish in the field experiments may have associated with groups of conspecifics and moved quickly out of the study area, thus escaping from predators in that area.

My experimental arena, while very large when considered in the context of similar laboratory efforts, limited the ability of my subjects to move more than 12 meters. The fish moved throughout the experimental arena, with their movement changing depending on the experimental conditions tested. When presented with unlimited range of movement in my field experiments, the majority of tagged and released fish moved out of the study area entirely. Both the lab and field studies indicate that juvenile cod move between small patches of eelgrass, and often spend large amounts of time in open areas while doing so. In the field, these results were particularly evident, as most juvenile cod moved out of the study area entirely. It

would appear that, while the factors identified above mediate the movement of juvenile cod outside of protective habitat, movement in highly fragmented habitat is high. This result has numerous implications for habitat-dependent behaviour and subsequent survival of juvenile Atlantic cod. Tethering studies have shown that predation risk on juvenile Atlantic cod is higher outside of eelgrass habitat (Linehan 2001) than inside it. If cod in highly fragmented habitat spend time moving between patches as my data suggest, they may experience higher mortality than fish moving in less fragmented habitat.

In addition to the potential for increased predation when moving between patches in highly fragmented areas, my research, combined with that of others, suggests that gaps in eelgrass habitat may have consequences for connectivity between juvenile cod inhabiting isolated patches of eelgrass. Studies by Sheppard (2005) and Laurel et al. (2003) indicated that movement rates in areas of continuous eelgrass were relatively low compared to the movement I observed in my study. These studies compared with my own research suggest that juvenile cod might be less likely to leave large patches of eelgrass, especially if the nearest patch is located a great distance away. Given this possibility, if fish are reluctant to cross open areas between large, suitable patches of protective habitat, connectivity between different groups (or populations) of cod might be limited at the juvenile level.

Additional work is required to determine the risk posed to juvenile cod of different sizes and densities of conspecifics as they move in open areas between patches of protective habitat. Further studies that examine movement between large areas of eelgrass separated by barren areas would be necessary to determine the

possibility of limited connectivity between such areas. The scale of my experiments was relatively small (approximately 10 m for my laboratory experiments and approximately 200 m for my field experiments), and may not reflect all of the scales of movement of these animals in the wild. It would be useful to conduct further field experiments at various spatial scales to determine at what scale gaps in habitat affect movement patterns. Use of PIT tags and sonar tracking would be useful in this regard, because they make it possible to determine exact locations of juvenile fish without recapture. Many components of fish behaviour, such as the capacity of fish to detect eelgrass patches at various distances, how they assess habitat suitability, the effects of tagging on their behaviour, and the specific effects of rapidly fluctuating group size are all further areas of study.

My thesis represents the first attempt to determine the effect of habitat gaps on movement of a marine species, and the factors that may mediate such movement. This work was based on movement studies of terrestrial animals, and suggests that concepts of movement corridors and isolation of animals in fragmented habitat can be useful for the management of marine systems as well. Eelgrass can serve as an important nursery habitat for juvenile cod during their juvenile life stage (Gotceitas et al. 1997, Laurel et al. 2003). The potential impact of eelgrass destruction, through either anthropogenic or natural means, on the movement behaviour of juvenile fishes has been partially addressed by my thesis, but requires further examination for understanding and effectively managing marine systems.

4.2 References

Baker, L. 2007. Effects of corridors on the jumping behaviour of the jumping spider *Phidippus princeps* (Araneae, Salticidae). Canadian Journal of Zoology 85: 802-808.

Barry, P.M., Carline, R.F., Argent D.G., Kimmel, W.G. 2007. Movement and habitat use of stocked juvenile paddlefish in the Ohio River system, Pennsylvania. North American Journal of Fisheries Management 27: 1316-1325.

Bosschieter, L., Goedhart, P.W. 2005. Gap crossing decisions by reed warblers (*Acrocephalus scirpaceus*) in agricultural landscapes. Landscape Ecology 20: 455-468.

Bright, P.W. 1998. Behaviour of specialist species in habitat corridors: arboreal dormice avoid corridor gaps. Animal Behaviour 58: 1485-1490.

Cote, D., Moulton, S., Frampton, P.C.B., Scuton, D.A., McKinley, R.S. 2004. Habitat use and early winter movements by juvenile Atlantic cod in a coastal area of Newfoundland. Journal of Fish Biology 64: 665-679.

Desrochers, A., Hannon, S. J. 1997. Gap crossing decisions by forest songbirds during the post-fledgling period. Conservation Biology 11: 1204-1210.

Gotceitas, V., Fraser, S., Brown, J.A. 1997. Use of eelgrass beds (*Zostera marina*) by juvenile Atlantic cod (*Gadus morhua*). Canadian Journal of Fisheries and Aquatic Sciences 54: 1306-1319.

Kopp, K., Wachlevski, M., Eterovick, P.C. 2006. Environmental complexity reduces tadpole predation by water bugs. Canadian Journal of Zoology 84: 136-140.

Laurel, B.J., Gregory, R.S., Brown, J.A. 2003. Settlement and distribution of Age-0 juvenile cod, *Gadus morhua* and *G. ogac*, following a large-scale habitat manipulation. Marine Ecology Progress Series 262: 241-252.

Lima, S.L. 1990. Protective cover and the use of space: different strategies in finches. Oikos 58: 151-158.

Lima, S.L., Wiebe, K.L., Dill, L.M. 1987. Protective cover and the use of space by finches; is closer better? Oikos 50: 225-230.

Linehan, J.E., Gregory, R.S., Schneider, D.C. 2001. Predation risk of age-0 cod (*Gadus*) relative to depth and substrate in coastal waters. Journal of Experimental Marine Biology and Ecology 263: 25-44.

Magurran, A.E., Irving, P.W., Henderson, P.A. 1996. Is there a fish alarm pheromone? A wild study and critique. Proceeding of the Royal Society of London B 263: 1551-1556.

Ng, C.L., Able, K.W., Grothues, T.M. 2007. Habitat use, site fidelity, and movement of adult striped bass in a southern New Jersey estuary based on mobile acoustic telemetry. Transactions of the American Fisheries Society 136: 1344-1355.

Rood, J.P. 1972. Ecological and behavioural comparisons of three genera of Argentina cavies. Animal Behaviour Monographs 5: 1-83.

Sheppard, G.L. 2005. Natural mortality and movement of juvenile cod (*Gadus* spp.) inhabiting eelgrass (*Zostera marina*) in coastal Newfoundland waters. MSc Thesis, Department of Biology, Memorial University of Newfoundland.

Sogard, S.M. 1997 Size-selective mortality in the juvenile stage of teleost fishes: a review. Bulletin of Marine Science 60: 1129-1157.

Thistle, M. E. 2006. Distribution and risk-sensitive foraging of juvenile gadids in relation to fractal complexity of eelgrass (*Zostera marina*) habitat. MSc Thesis. Memorial University of Newfoundland, St. John's, NL.

Tupper, M., Boutilier, R.G. 1997. Effects of habitat on settlement, growth, predation risk and survival of a temperature reef fish. Marine Ecology Progress Series 151: 225-236.

Zollner, P.A., Lima, S.L. 1999. Illumination and the perception of remote habitat patches by white-footed mice. Animal Behaviour 58: 489-500.